

**LANDSCAPE EVOLUTION IN WESTERN AMAZONIA: PALYNOSTRATIGRAPHY,  
PALAEOENVIRONMENTS AND DIVERSITY OF THE MIOCENE SOLIMÕES  
FORMATION, BRAZIL**

**By**

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A thesis submitted to the University of Birmingham  
for the degree of DOCTOR OF PHILOSOPHY

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Environmental Sciences  
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June 2016

# UNIVERSITY OF BIRMINGHAM

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## ABSTRACT

During the Miocene (23.03 to 5.33 Ma), western Amazonia experienced major changes in its geography and biodiversity as a response to Andean uplift. To better understand these changes, the palynology of the Solimões Formation (NW Brazil) is presented with the objective of providing age control, and establishing palaeoenvironments and pollen richness within the framework of geological and climatic events. The ninety-five palynological samples yield 491 palynomorphs, of which 76 pollen and 25 spores are new. Correlation with a nearby calibrated biozonation resulted in ages from 18.7 to 10.7 Ma (late early to earliest-late Miocene). The pollen associations are typical of Amazonian humid forests, with abundant palms, Bombacoideae, trees and grasses, and lack diverse and abundant herbs or dry forest indicators. Spikes in algae and dinoflagellates show phases of lake development and two marine incursions – one between 18.4 and 17.8 Ma, and another between 14.1 and 13.7 Ma. Statistical analyses of the data show inundations had no effect in the vegetation composition. Estimates of diversity using different metrics clearly show a diversity increase and community change at ca. 16 Ma, independent of lithofacies. This change is driven by the Middle Miocene Climatic Optimum and not correlated with any of the marine incursions. Altogether, the results bring more detail to the environmental history of western Amazonia, establishing two inundation events and furthering the climate-diversification relationship in Neotropical biomes into the Miocene period.



To my family and teachers.

## **ACKNOWLEDGMENTS**

Many thanks to:

-My supervisor Guy Harrington for his constant support, patience and source of ideas throughout these years.

-Carlos Jaramillo, with whom I initially formulated the PhD idea and who helped me with many aspects of my work.

-The Geological Survey of Brazil (CPRM), Fernando Burgos and Gert Woeltje (DNPM-Manaus) for access and sampling permits.

-Vladimir Zapata, who spent a very hard-working month describing and sampling sediment cores with me in the heat of Manaus.

-Frank Wesselingh and Stephen Louwye for help with identification of molluscs and dinoflagellates, respectively.

-Ingrid Romero, Silane Silva Caminha and Fátima Leite for their previous works, shared data and many discussions on the taxonomy of pollen and spores from the Amazon.

-Mario Vicente Caputo and Emílio Amaral, for sending papers/reports and for many discussions on aspects of the geology of the Amazon basin.

-Aruna and Gretchel (Earth Sciences, UoB) for their help with facilities and paperwork in the department.

-John Ortiz for his brilliant work producing stratigraphic logs using R codes!

-James Bendle, Frederike Wittkopp and Heiko Moossen for their help teaching me and providing ideas for geochemistry work.

-Jon Sadler for his role as second supervisor.

-Tom Dunkley-Jones and Alejandro Machado for trying to find nannofossils and foraminifera in my samples, unfortunately they didn't.

-All the staff and colleagues of Earth Sciences, for the nice environment created, coffee mornings, field trips, paper clubs, supervision groups, and also some pub time eventually – cheers!

-All my friends in Birmingham, life would have been much harder without them – thank you!

- My housemates Plamen, Simiao and Mayra for sharing a house and many great times together!
- Agno Acioli, Ronaldo Almeida, Miranda, Seu Nixon and the staff of Universidade Federal do Amazonas in Benjamin Constant for their support during field work.
- Suzette Flantua for sharing data from the Latin American Pollen Database.

I am grateful to the following for funding:

- CAPES (Coordenação de Aperfeiçoamento de Pessoal em Nível Superior) for the scholarship that allowed me to be abroad for my studies. And also thanks to Maria L. Absy who was my tutor for this scholarship application.
- ASSP (American Association of Stratigraphic Palynologists) for a small research grant and a travel grant that helped me having lab work finished and attending an international conference.

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### **CD (enclosed on inside back cover)**

1. Excel sheet with raw pollen counts of core 1-AS-105-AM;
2. Excel sheet with all cores and depths used to build isopach map;
3. Text files (.txt) used for the age model (to accompany R codes for age model);
3. All R code as .rtf files;
4. Excel sheet with raw data organised for CCA analysis and for producing pollen diagrams.

**Total word count: 43,026**

**(Excluding tables and figure captions)**

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## Chapter 1: Introduction

### 1.1 The Miocene World

The Miocene spans from 23.03 to 5.33 million years (Gradstein *et al.* 2012) (Fig. 1.1) and is characterised as an interval of global cooling that nevertheless still had predominantly warmer temperatures than present day (Zachos *et al.* 2001, 2008). This represented a continuation of a long-term cooling trend from the mid Eocene, but punctuated by a climatic optimum that took place at the middle Miocene, known as the Mid-Miocene Climatic Optimum (MMCO; ca. 17 to 15 Ma, Zachos *et al.* 2001). The estimated temperatures for this event are approximately 3° to 4 C° higher than today (You *et al.* 2009, Goldner *et al.* 2014) and therefore they could represent a close analogue to postulated climate scenarios for the next one or two centuries (IPCC 2014), making the event of particular interest for palaeoenvironmental studies. Following the MMCO, global conditions entered a progressively cooling phase referred to as the Middle Miocene Climatic Transition (MMCT). As with other periods of palaeoclimatic history, the temperature trend of the Miocene seems to be coupled with fall of atmospheric carbon dioxide levels (from 400-500 ppmv or more around the MMCO to 300 ppmv or less at the late stages of the Miocene; Fig. 1.1., Beerling and Royer 2011, Foster *et al.* 2012, Zhang *et al.* 2013). There is still considerable debate on the relation of CO<sup>2</sup> and temperature during the Miocene, a debate driven by studies that show a decoupling of these variables (e.g. alkenone derived SST, LaRiviere *et al.* 2012), and modelled warmth estimates requiring CO<sub>2</sub> concentrations of ca. 800 ppmv (Goldner *et al.* 2014), which are significantly higher than most reconstructions. Nevertheless, the relationship seems to hold (Beerling and Royer 2011) as supported by newly available alkenone records (Zhang *et al.* 2013), boron isotope (Foster *et al.* 2012), and leaf stomatal reconstructions (Kürschner *et al.* 2008).

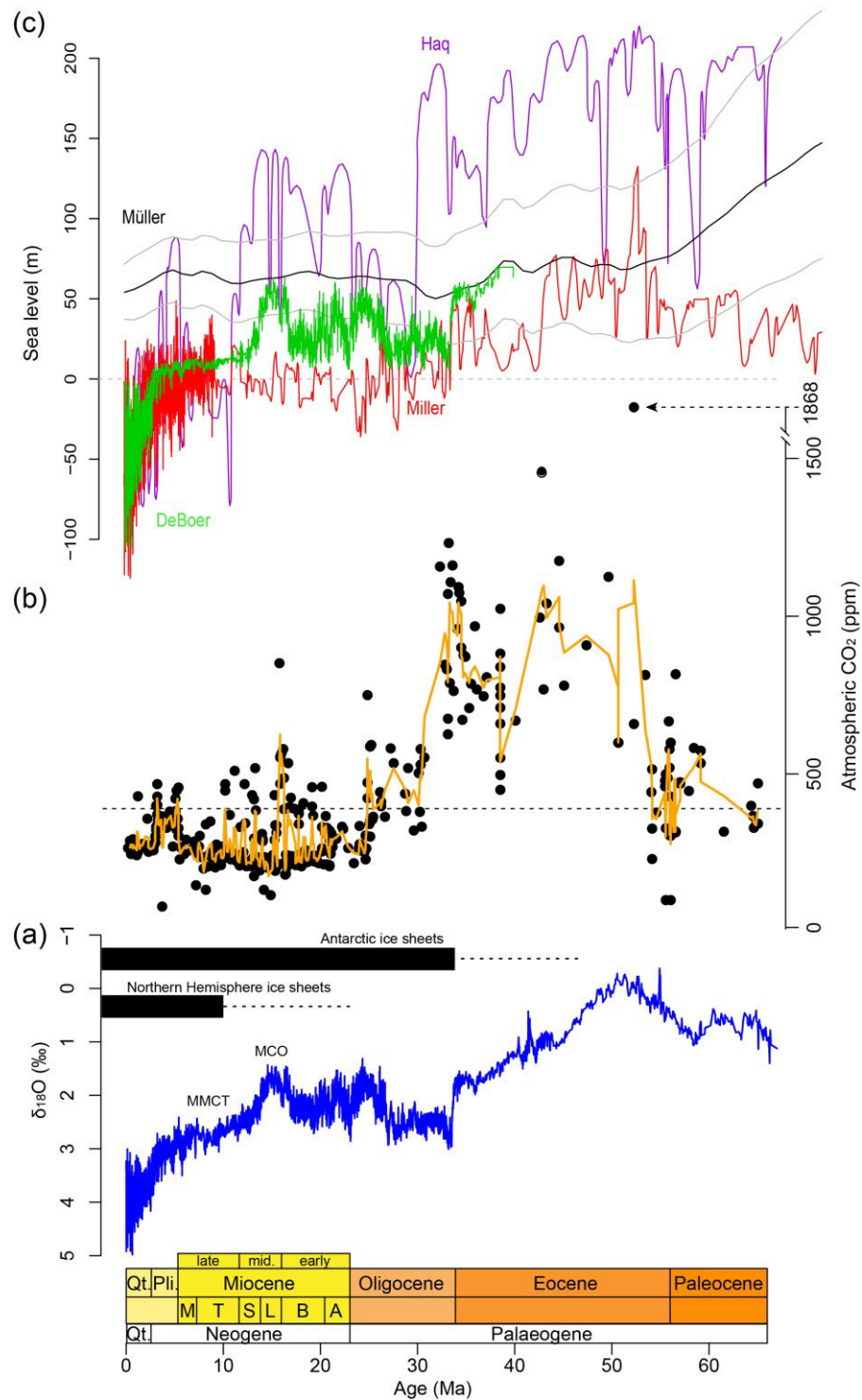


Figure 1.1. Palaeoclimatic proxies and sea level estimates for the Cenozoic. Panel a):  $\delta^{18}\text{O}$  from benthic foraminifera (Zachos *et al.* 2001, 2008) used as a temperature proxy; Miocene stages, M: Messinian, T: Tortonian, S: Serravalian, L: Langhian, B: Burdigalian and A: Aquitanian. Panel b): Atmospheric CO<sub>2</sub> (ppm) estimates derived from stomate, phytoplankton, palaeosols, liverworts, Boron and B/CA (data compiled by Beerling and Royer 2001), dotted line is present-day CO<sub>2</sub> cc (390 ppm). Panel (c): global sea levels estimates (Haq *et al.* 1987, Miller *et al.* 2005, Müller *et al.* 2008 and DeBoer *et al.* 2010).

As a result of the temperature evolution and its direct influence on ice volume stored on land (Foster and Rohling 2013), sea levels also fluctuated (Fig. 1.1). Despite estimation uncertainties and inconsistencies among published records, most studies seem to agree that the sea level throughout or intermittently during the Miocene was higher than present (Haq *et al.* 1987, Miller *et al.* 2005, Müller *et al.* 2008, DeBoer *et al.* 2010) and somewhat mirrored benthic  $\delta^{18}\text{O}$  data (Zachos *et al.* 2001) and temperature estimates (DeBoer *et al.* 2010, Beerling and Royer 2011). This implies that sea levels were at their highest levels during the MMCO (ca. 50-60 metres a.s.l., Fig. 1.1), and subsequently started to drop steadily in response to cooler climatic conditions. The climatic evolution also translated into changes in ice caps on both North and South poles. Antarctic has been glaciated since ca. 34 Ma ago, but it was during the middle Miocene that a permanent ice cover developed in east Antarctic (Shackelton and Kennett 1975). In the northern hemisphere ice sheets have existed at least since the late Miocene (but probably as early as the middle Miocene; Wright 1998, Zachos *et al.* 2008), and it was during the Miocene that bipolar glaciations started. All these climatic changes had a worldwide effect on the distribution of vegetation, following the long-term cooling trend forests were beginning to adapt to colder temperatures that have persisted since the early Miocene. Nonetheless, a warmer than present world meant current biomes could be present at higher latitudes, for instance following the MMCO cool-temperate forests existed in the high north, warm-temperate mixed forests in mid-latitudes and shrubby tundra in Antarctica (Pound *et al.* 2012). These vegetation types were gradually narrowing their distribution as the world got cooler, tundra disappeared from Antarctica by the late Miocene and taiga developed in the high north (Pound *et al.* 2012). In the equatorial Neotropics, broadleaf evergreen forests have existed since the early Miocene (Hoorn 1993, Hoorn *et al.* 2010, Silva-Caminha *et al.* 2010, Jaramillo *et al.* 2014), and by the late Miocene dry biomes

have appeared for example in the Patagonian steppe (Palazzesi *et al.* 2014), the cerrados of central Brazil (Simon *et al.* 2009), and savannahs/deserts worldwide (Pound *et al.* 2012).

Ocean currents during the Miocene underwent important shifts that made them nearly as they are today. From early to middle Miocene, plate rearrangements caused the closure of the Tethys ocean (Okay *et al.* 2010) and the Indonesian gateway (Kuhnt *et al.* 2004), and the rise of the Panama isthmus (Coates *et al.* 2004, Montes *et al.* 2015) resulting in the termination of the circum-equatorial current and its replacement by the subtropical Pacific and Atlantic ocean gyres as well as a strengthened Gulf stream (Potter and Szatmari 2009). Middle Miocene opening of the Greenland-Scotland ridge affected the North Atlantic by controlling the input of arctic cold waters (Wright and Miller 1996, Wright 1998). All these changes transformed the global oceans currents and had impacts on the climate and consequently on biome distributions on the planet as a whole. In terms of landscape, continental configurations underwent important transformations, and in the middle to late Miocene major mountain chains like the Himalayas (Powell and Conaghan 1973, Copeland and Harrison 1990) and the Andes (Hoorn *et al.* 2010) had accelerated rates of uplift. By late middle to late Miocene overall continental distribution was nearly that of the present-day (Potter and Szatmari 2009).

## **1.2 The Amazon Basin**

The Amazon craton is one of the oldest pieces of continental crust on Earth, with basement rocks dating back to Precambrian times (Wanderley-Filho *et al.* 2010). The craton migrated west after the break-up of Gondwana to form the core of South America (Scotese 2009), which then drifted away from the African continent from the Triassic onwards, remaining an isolated landmass from middle Cretaceous (ca. 100 Ma) until the closure of the Panama isthmus in the Miocene ca. 13 to 15 Ma ago (*sensu* Montes *et al.* 2015).

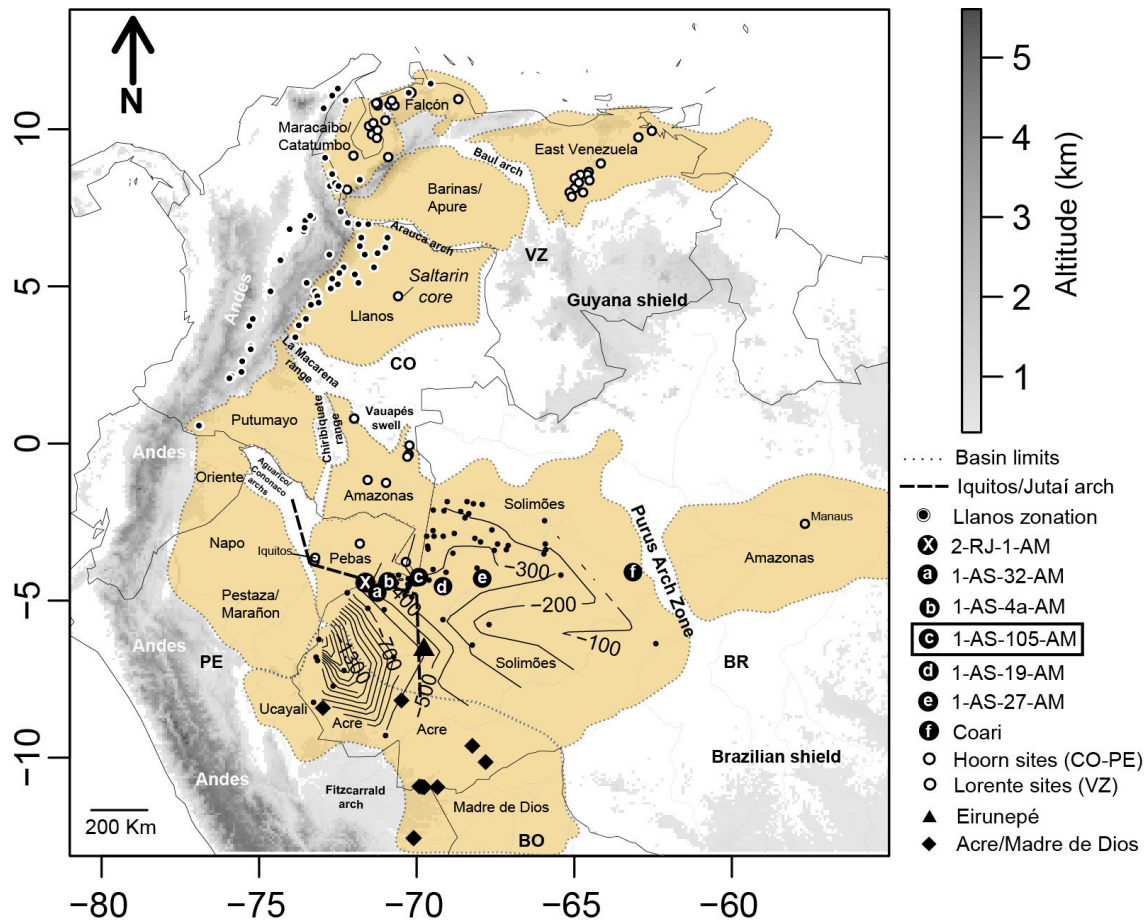


Figure 1.2. Map of NW South America with all sites cited in this thesis. Basin names are within the limits drawn with dotted lines. Sites in the Llanos basin and surroundings are part of the Llanos and Llanos foothills pollen zonation of Jaramillo *et al.* (2011); Sites in Venezuelan basins are part of the pollen zonation of Lorente (1986) and sites in Colombian and Peruvian Amazonas basin are from studies by Hoorn (1993, 1994a, 1994b). Letter X (2-RJ-1-AM) is Solimões type section (Eiras *et al.* 1994); Letters (a to f) in the Solimões basin are as follow: a) core 1-AS-32-AM (Latrubesse *et al.* 2010), b) core 1-AS-4a-AM (Hoorn 1993), **c) core 1-AS-105-AM (this work)**, d) and e) cores 1-AS-19-AM and 1-AS-27-AM, respectively (Silva-Caminha *et al.* 2010), f) outcrops around Coari city (Nogueira *et al.* 2013). Solid triangle is outcrops close to Eirunepé city (Gross *et al.* 2011); solid diamonds are Acre/Madre de Dios sites of Latrubesse *et al.* (2010). Isopach lines were plotted using formation thickness measured in 107 boreholes (small solid circles scattered around Solimões basin including sites X, a, b, c, d and e) from the Brazilian Geological Survey (CPRM) and Petrobrás, data was linearly interpolated using R package Akima. Positions of basins and arches after Hoorn (1993), White *et al.* 1995, Roddaz *et al.* (2005), Mora *et al.* 2010, Montenegro and Barragán (2011), Sarmiento (2011) and Kroonenberg and Reeves (2011). DEM plotted is  $\geq 300$  m derived from ETOPO 1 (Amante and Eakins 2009). BR: Brazil, BO: Bolivia, PE: Peru, CO: Colombia, VZ: Venezuela.



The Amazon hydrographic basin is an intracratonic feature that extends from the Andes in the west to the Atlantic coast in the east. It is bounded by the Guyana shield to the north, and the Guaporés, or Central Brazil, shield to the south (Fig.1.2). Basin infill has developed since early Palaeozoic times, including phases of glacial and marine sedimentation in the Ordovician–Upper Cambrian, and marine to continental in the Meso-Cenozoic (Eiras *et al.* 1994). From the Late Cretaceous sedimentation was influenced by mountain building in the west associated with the Andean chain. The basin is divided by structural arches along its E-W axis (Fig.1.2). The western basins harbour sequences of sediments that accumulated in continental and marginal marine environments with clastic supply from the Precambrian shields, and increasingly from the Andes as it uplifted. The Andean orogeny resulted in the cessation of river flow to the west, which drained the area to the Pacific Ocean in the Palaeogene, and in the gradual development of a low energy system of meandering rivers, lakes and swamps, which had its maximum development during the Neogene (Miocene plus Pliocene, i.e. 23.03 to 2.59 Ma), when a vast wetland covered the western Amazon (Wesselingh *et al.* 2002, Hoorn *et al.* 2010). It was also during the Neogene that the Andes had its last major uplift, an event that drastically changed the drainage system and culminated in the formation of the Amazon River that began flowing east from late Miocene (Figueiredo *et al.* 2009, Sacek 2014).

Today Amazonia extends over ca. seven million km<sup>2</sup> in nine different countries and it is the largest tropical forest on the planet, with a key role in influencing the global climate (Goulding 2003). The region is a major component of the global carbon cycle, producing ~20 Pg C/year by photosynthesis, accounting for ~20% of global terrestrial carbon cycling (ca. double annual fossil fuel emissions) and holding ~25% of terrestrial biomass (Grace *et al.* 2001), a number that is ca. 86 Pg C (Saatchi *et al.* 2007). It is also a principle component of the global hydrological cycle — the Amazon River accounts for ~20% of all the freshwater

discharged into the world's oceans (Franzinelli and Potter 1984). Along its course from the Andes to the Atlantic Ocean, it runs ca. 6.700 km and connects to tributaries that are amongst the largest rivers on the planet (e.g. the Madeira and Purus Rivers) (Goulding 2003). Precipitation is high almost across the entire basin and is primarily controlled by the Intertropical Convergence Zone, which brings moisture to the hinterland from the tropical Atlantic. Rainfall is higher in the western Amazonia, where months with precipitation <100 mm does not exist in vast areas that are thus non-seasonal (Sombroek 2001). A huge amount of water is recycled in the basin through the precipitation/evaporation cycle (up to 50%) (Salati and Vose 1984, van der Ent *et al.* 2010); the associated evapotranspiration vents latent heat into the atmosphere, contributing to the largest land-based atmospheric convection centre on Earth with connections to extra-tropical hydrology and circulation (Barry and Chorley 1995).

In terms of biodiversity, Amazonia has always called the attention of scientists for its high and partially unexplored diversity. After decades of collection, even large mammals are found in recent times like the newly described titi monkey (Dalponte *et al.* 2014), as well as several bird species (Miranda *et al.* 2013), not to mention the more often new plant species (e.g. Campacci *et al.* 2010, Koch *et al.* 2013). Diversity estimates of plant species richness have been ongoing for many decades and usually involve the counting of trees in forest plots (Black *et al.* 1950, Pires *et al.* 1953), and because of the high number or rare species these estimates rely on statistical modelling. Numbers vary from over 11,000 to 16,000 trees >10 cm DBH (diameter at breast height) (Hubbell *et al.* 2008, Steege *et al.* 2013), to overall plant diversity between 30,000 and 80,000 (numbers are quite variable due to sampling gaps and herbaria misidentification or lack of identification, Hopkins 2007). A general pattern has been found and shows a gradient of increasing diversity from east to west (Morales and Vinicius 2003, Steege *et al.* 2006), that seems to follow rainfall, soil fertility and ecosystem

productivity. The diversity of Amazon plants is spread along a vast area of lowland that, contrary to long held views, is highly heterogeneous. Various types of habitats exist (Fig. 1.3): the *terra firme* forest is the upland type, covering up to 90% of the land, not prone to flooding, the most diverse, with a higher canopy and relatively clear understory (Pires 1974, Schubart 2000). This forest also has specific vegetal formations like those dominated by lianas, palms, bamboo and in ecotone regions it can acquire a dryer than normal appearance (Pires and Prance 1985). The second most important type of vegetation is the seasonally flooded forests, divided in whitewater (*várzea*) and blackwater (*igapó*) forests. *Várzeas* are flooded by rivers originating in the Andes that carry a heavy sediment load and therefore are rich in nutrients. *Igapós* are flooded by low nutrient waters washed from inside forests and rich in humic acids from leaf decomposition, like those of the Negro River (Prance 1978, Pires and Prance 1985, Wittmann *et al.* 2002, Junk *et al.* 2011). Scattered around and in lower proportion there are savannah and *campina* forests – savannahs are restricted to bordering areas where dryer climates prevail like in the northern Brazilian state of Roraima. Campinas are heath forests, present all over the basin and having an edaphic constraint in their development, poor soils composed largely of white sand and sometimes waterlogged (Adeney *et al.* 2016). Contrary to *terra firme* and flooded forests, savannahs and *campinas* have a low stature in their physiognomies, they differ from each other in that savannahs can have a dense grass cover but campinas do not (Pires and Prance 1985, Ferreira 2009). This diversity in habitat types increases the number of endemic species and in turn the overall plant diversity in Amazonia.

A matter of constant debate is the origin of diversity in Amazonia. When and how did so many species originate? What is the relation of climate, ecology, geography and other variables in triggering speciation? Hypotheses have existed for over a century, and started as old as in 1878 when Alfred R. Wallace postulated that the long term stability of the

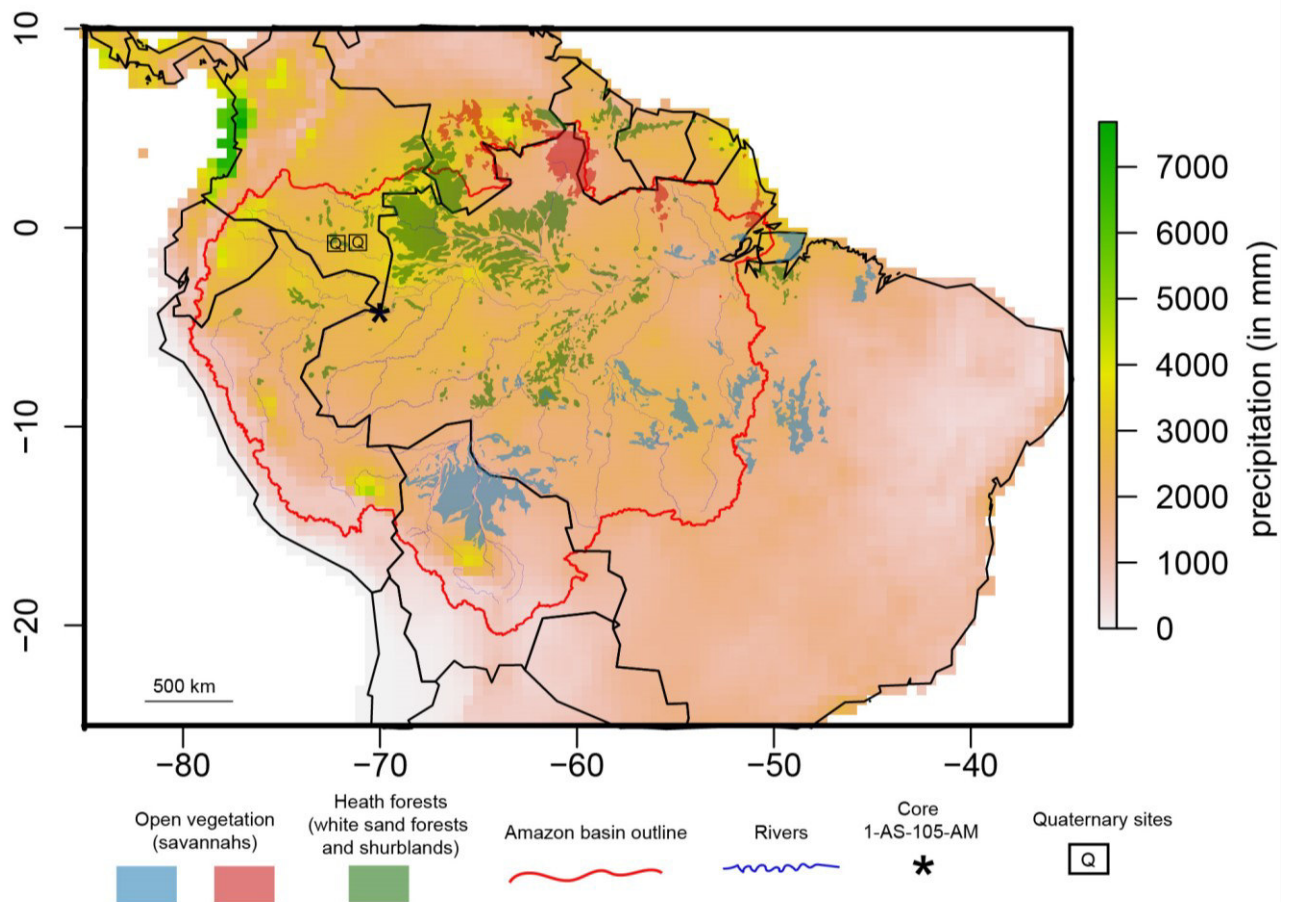


Figure 1.3. Map of NW South America with mean annual precipitation (coloured background) and limit of the Amazon hydrographic basin (red line). Vegetation types are shown for the area within the red line and close surroundings only. Dense evergreen forest (*terra firma*) covers the majority of the area (not shown in any colour, for clarity) and small patches of other main vegetation types are shown in blue (savannahs), red (savannahs including highland open areas of the Guyana mountains) and green (white-sand formations); see texts for details. Flooded forests (*várzea* and *igapó*) are associated with the main rivers (thin blue lines). Background map produced using R package ‘*dismo*’ (Hijmans *et al.* 2013) and vegetation adapted from Adeney *et al.* (2016).

ecosystem would create appropriate conditions for the gradual accumulation of species. In that regard, tropical areas are museums, where low extinction rates (Stebbins 1974) lead to increments to the species pool as time passes by. Not only are tropical areas museums, but also cradles where animals and plants originate and subsequently spread to and adapt in extratropical areas (Davis *et al.* 2002, Jablonski *et al.* 2006, 2013; Antonelli *et al.* 2015). The birth of tropical diversity posits two main types of questions, the first about mechanisms and the second about timing of species originations. Mechanisms leading to diversity in the tropics can be associated with a variety of factors like (i) biotic relationships (Dobzhansky 1950, Vermeij 2005, Schemske *et al.* 2009) and to (ii) expansion of the available area that species occupy (Rosenzweig 1995, Fine *et al.* 2008). Timing of diversification is a more tractable topic that can be studied using the fossil record as well as genetics. Using dated phylogenies and fossil calibration of typical understory plants from the Neotropics, Davis *et al.* (2005) postulated a mid-Cretaceous origin for the tropical forest structure. Perhaps with more certainty, a modern-like plant association started existing in the Paleogene ca. 58 Ma, as revealed by the Cerrejón Coal deposits of Colombia, where many affinities were established between extant plant families and Paleogene macrofossils (Wing *et al.* 2009). Following this first record of a tropical forest, no fundamental changes to the structure and composition of plant diversity have been recorded, and dominant families seem to have since then been the same all around the tropics (Ricklefs and Renner 2012). Irrespective of a relatively stable tropical forest during the past ca. 60 Ma, diversity oscillates constantly and this oscillation does not seem to occur randomly. Temperature is thought to be a key player in driving plant diversity - plant communities responded to warming periods of the Tertiary by promoting diversification (Jaramillo *et al.* 2006, Jaramillo *et al.* 2010b). Overall neotropical plant diversity seems to mirror global temperature records, with peaks of diversification during peaks in temperature, e.g. the PETM (Paleocene-Eocene Thermal Maximum) and decreases

during cooling periods like the Oligocene. Direct and important conclusions of this story are that (i) there is a directionality in plant diversity over time closely related to climate and (ii) tropical forests already experienced much higher temperatures without collapsing (e.g. Dick *et al.* 2013).

### **1.3. The Miocene of western Amazonia**

During the Miocene, the Amazon basin largely acquired a modern geography. The basin's dimensions were similar to present, except in early to middle times of the Miocene when west Amazonia was connected to the Orinoco, Magdalena and north Paraná drainages (Lundberg *et al.* 1998). These Pan-Amazonia connections were possible because Andean deformation was not yet developed enough to generate the water-shed divides that later isolated basins (Mora *et al.* 2010). As a result of lower topographic ranges in the Andean chain during the early to earliest middle Miocene, drainage developed in cratonic areas (e.g. Guyana shield) with a westward flow into western Amazonia, and sediment accumulation developed along the Andean south-north stretching basins and east-west intracratonic basins (Hoorn *et al.* 2010). This drainage system was also flowing north into the Orinoco and subsequently into the Caribbean Sea, from which marine incursions advanced against the continent at times (Vanhof *et al.* 1998, Hovikoski *et al.* 2007, 2010, Linhares *et al.* 2011, Boonstra *et al.* 2014, Jaramillo *et al.* in prep (this thesis chapter 6 and appendix)). This vast area had a very low topographic gradient, rivers flowed slowly and because of that vast lakes (a.k.a. 'Pebas system') were formed and persisted for thousands to millions of years (Hoorn 1993, 1994a, 1994b, 2010, Wesselingh 2002, 2006, Wesselingh *et al.* 2006c) during the early and middle Miocene. During the late Miocene, a peak in Andean orogeny at ca. 12 Ma intensified sediment infilling of the Andean foreland basins (Uba *et al.* 2007) that eventually

became overfilled and therefore the wetlands had their demise (Wesselingh *et al.* 2002, Hoorn *et al.* 2010).

The late Miocene in western Amazonia is characterised by more river dominated environments (Westaway 2006, Latrubesse *et al.* 2007, 2010, Silva-Caminha *et al.* 2010, Gross *et al.* 2011). With accelerated basin infill generated by continued uplift of the Andes, large-scale accretion processes advanced eastward until the central Amazonia Purus arch was breached (Sacek 2014). Expression of this evolution is recorded at the Amazon Fan, with replacement of the carbonate platform with more terrigenous sediments from ca. 11.8 Ma (Figueiredo *et al.* 2009), suggesting the onset of the reversed drainage at this point of time. By the latest late Miocene and Pliocene, important rivers disconnected from the Andes as a result of local uplifts (Latrubesse *et al.* 2010), like the Fitzcarrald and Vaupés highs (Fig. 1.2) (Mora *et al.* 2010). This led to the final reorganisation of the transcontinental Amazon drainage system.

### ***Biodiversity***

The evolution of the Amazon biota follows the story narrated above. The Pebasian wetland was inhabited by a diverse molluscan fauna that included an outstanding number of endemics (Nuttall 1990, Wesselingh 2006). Lakes and rivers also witnessed the diversification of a rich fish fauna (Monsch 1998, Lundberg *et al.* 2010), part of which invaded western Amazonia from the Caribbean during marine connections (Lovejoy *et al.* 1998, 2006, Cooke *et al.* 2011). This invasion includes the river dolphin (Hamilton *et al.* 2001). Large mammals and reptilians also lived in and around the Miocene wetlands, like crocodilians and rodents (Kay *et al.* 1997, Cozzuol 2006, Latrubesse *et al.* 2010), among others. One of the most extraordinary megafaunal records has been the apex predator *Purussaurus brasiliensis* that reached over 12 metres long and had a bite force comparable to

that of a *Tyrannosaurus rex* (Aureliano *et al.* 2015). The great majority of this fauna went extinct by the Late Miocene and Pliocene, when the wetlands drained. At ca. 10 Ma, the intensification of the Great American Biotic Interchange (GABI) brought completely new elements to the faunal diversity of western Amazonia from central and north America (Carrillo *et al.* 2015).

Knowledge of Miocene plant diversity in western Amazonia greatly depends on palynology. To date, known botanical affinities of Miocene pollen and spores is scarce, but nevertheless allow us to have a picture of palaeovegetation. Tropical evergreen forest has existed over the entire Miocene with no change in biome type (Hoorn *et al.* 1993, 1994a, 1994b, Silva-Caminha *et al.* 2010). What is more, the continuous and frequent presence of abundant palms, Bombacoideae, grass and aquatic plants pollen in sedimentary sequences attest to the presence of flood plains (*várzeas*) and swamps. Some authors (Hooghiemstra and Van der Hammen 1998, Van der Hammen and Hooghiemstra 2000, Jaramillo *et al.* 2006) have used pollen counts from west Amazonia sites to tentatively compare them to similar modern sites and suggested that plant diversity may have been higher in the Miocene. Other attempts found no significant difference between Miocene and extant pollen diversity (Jaramillo *et al.* 2010a). Most importantly there is a complete lack of a comprehensive Miocene pollen diversity analysis that details how diversity changed over time and the relationship to other extrinsic variables.

## **1.4 Objectives of the present thesis**

1.4.1 To improve the Neogene biostratigraphy of western Amazonia by means of performing palynological analyses of borehole samples. Regional palynostratigraphy is entirely dependent on correlation with pollen zonations in Venezuela and Colombian Llanos (Lorente 1986, Jaramillo *et al.* 2011). A need for more robust biostratigraphical frameworks



exists. Hence detailed palynological work must seek to improve the number of correlative points (key species) used basinwide. This is done by means of dating one core (Chapter 5) and fully describing its palynology, including new species (Chapter 4).

1.4.2. To identify marine incursions during the time of deposition studied (Chapter 6). Due to the fairly low-angle deposition and dense vegetation cover, studied outcrops are short sections over long geographic distances. This in turn significantly hampers correlation of strata and as a result mapping and timing of marine incursions has been very contentious (e.g. Hovikoski *et al.* 2010 and Latrubesse *et al.* 2010). How many times did brackish or marine water reach western Amazonia? What was the duration of such incursions? The null hypothesis of non-existence of such marine incursions is ruled out due to well-known episodic incursions (Hoorn 1993, Linhares *et al.* 2011).

1.4.3. Marine incursions potentially were major disturbances to the environment in a large basin-wide scale, yet little is known about vegetation responses to these disturbances. Are there differences in the floristic composition before and after marine incursions? Did they cause origination or extinction? (Chapter 6 and 7).

1.4.4. Does plant diversity correlate with global temperature? (Chapter 7). Following existing patterns shown by Jaramillo *et al.* (2006, 2010b), species diversity correlates positively with temperature change, thus showing increase in biodiversity during warm periods. Conversely, temperature change could promote extinction, or diversity is steady over time. The Neogene has a well-known temperature trend, with a thermal maximum during the mid Miocene, and then a decreasing pattern towards the Quaternary (see Fig. 1.1).

## Chapter 2: Study site

### 2.1 Introduction

Miocene deposits in Amazonia can be found covering a wide geographical area. In central parts of Amazonia, the Novo Remanso Formation (Dino *et al.* 2012) (Amazonas basin in Fig. 1.2) harbours unknown thicknesses of Miocene sediments that accumulated in fluvial settings most likely in isolation from western Amazonian areas (Dino *et al.* 2012, Nogueira *et al.* 2013). Sediments of the Novo Remanso lack a good mapping of their extension and morphology and also facies suitable for pollen analysis are rather rare. In western Amazonia, on the other hand, the Solimões Formation harbours a thick package of early to late Miocene deposits (see chapter 5) accumulated in paralic settings like those of the Pebas System of lakes and megalakes (Wesselingh *et al.* 2006, Hoorn *et al.* 2010), and its morphology is much better understood (e.g. Maia *et al.* 1977, Latrubesse *et al.* 2010). Many studies have shown thick and flat sequences of pollen rich sediments with a wealth of diversity and possible marine connections with the Caribbean area as indicated by marine palynomorphs and other structure and fossil forms (Hoorn 1993, Silva-Caminha *et al.* 2010, see chapter 6 for a more detailed account).

### 2.2 Solimões Formation

The Solimões Formation in Brazil is located within the Solimões and Acre basins (Fig.1.2). It extends laterally to neighbouring countries with different names: to the northwest in Colombia (Amazonas Formation), to the west in Peru (Pebas Formation), and to the southwest and south in Peru and Bolivia (Ucayali and Madre de Dios, respectively). This entire system is bounded north and south by high topographic domains, namely the Guyana and Brazilian shields formed of Precambrian basement rocks. To the east, a structural high called the Purus Arch is the boundary, although doubts remain towards the real tectonic

activity of this structure during deposition of the Solimões Formation (Caputo 2011). To the west, the Iquitos Arch is a divide that separated the Solimões/Pebas system from other Andean foreland basins (Fig.1.2), and that at least partially affected regional deposition - the position and activity of this arch are still debated (e.g. Latrubesse *et al.* 2010). Other smaller structures also play a role in the spatial configuration detailed above, their locations can be seen in Fig.1.2. The Formation overlies the Paleocene-Miocene Alter do Chão Formation in the east and the (possibly) Paleocene Ramón Formation in the west, and is overlain throughout the basins by the Pleistocene Içá Formation, modern fluvial sediments or it crops out (Caputo 1973, Maia *et al.* 1977). The Solimões type locality was proposed by Eiras *et al.* (1994) from core 2-RJ-1-AM (Fig.1.2). Sediments accumulated predominantly in fluvio-lacustrine environments and the lithology found is that of grey to green muds and clays, silts, sands and, less abundantly, layers of lignite and rarely limestone. Age relies most heavily on biostratigraphy (mammals, reptilians, molluscs and palynology) due to the lack of other dating means. Early Miocene to Pliocene ages have been established, however, there is some degree of uncertainty especially regarding spatial variability of these ages.

Borehole data from the Brazilian Geological Survey (CPRM) and Petrobras were used to create an isopach map (Maia *et al.* 1977, Latrubesse *et al.* 2010, and Fig.1.2). It shows the depocentre of the Formation is located in the Acre region, westward the Arch of Iquitos, with depths of up to 2,000 metres. This configuration has been used to suggest that sedimentation was spatially influenced by the Iquitos arch (Latrubesse *et al.* 2010). The Brazilian geological service and a series of researchers worked in the Solimões and Içá Formations with the aims of detailing age, modes of deposition, paleoenvironments and paleogeography of this vast area (Maia *et al.* 1977, Couto 1981, Frailey, 1986, Hoorn 1993, Hoorn *et al.* 2010, Latrubesse *et al.* 1997, 2007, 2010, Nuttall 1990, Räsänen *et al.* 1995, Monsch, 1998, Vonhof *et al.*

2003, Hovikoski *et al.* 2005, 2007, 2008, 2010, Westaway, 2006, Wesselingh, 2006 Cozzuol, 2006, Silva-Caminha *et al.* 2010, Linhares *et al.* 2011, Gross *et al.* 2011).

## **2.3 The ‘Carvão no Alto Solimões’ project**

Along the upper reaches of the Solimões River, thin layers of coaly sediments like lignite can be found in outcrops. A coal prospection project in the mid-seventies, the ‘Carvão no Alto Solimões’ (*Upper Solimões Coal*) was performed by the Brazilian Geological Survey (Maia *et al.* 1977). Eighty-four cores were retrieved using rotatory diamond drilling with H diameter (top 20 metres), N diameter (up to 200 metres) and B diameter (deeper than 200 metres). The cores are stored in Manaus, Brazil, at the facilities of DNPM (Departamento Nacional de Pesquisa Mineral, ‘National Department for Mineral Production’) and CPRM (Companhia de Pesquisas em Recursos Minerais, ‘Mineral Resources Research Company’).

### **2.3.1. Core 1-AS-105-AM**

Many of the cores from the Solimões project were damaged because of poor storage conditions, but some remain in good state of preservation. Among those, core 1-AS-105-AM was not only well preserved but also in a strategic position: it is between cores 1-AS-4a-AM (Hoorn 1993) and 1-AS-27-AM (Silva-Caminha *et al.* 2010), which are of early to early-middle Miocene and late Miocene ages, respectively, and therefore a good coverage of the middle Miocene could be advanced, which was essential to answer the research questions here proposed. Core 1-AS-105-AM is located in the vicinity of Tabatinga, Brazil (-4.5, -69.933), it reached 405.2 m and had a total recovery of 271.14 m. The top 26.2 m were discarded at the drilling site, as they were composed of recent fluvial sandy deposits of no interest at the time. The core is composed almost entirely of the Solimões Formation, from 26.2 to 332.7 m, and the remaining 72.5 m are described as Ramón Formation. A summary

core log is presented here (Fig. 2.1) and a detailed log is attached to the appendix material of this thesis (Fig 9.4). Overall, sediments of the Solimões Formation in this borehole are poorly consolidated, mostly massive, with few preserved structures or bioturbation. Fossil content is seen as fragmented carbonized plant remains of millimetric scale, fragmented shell bits but also some layers with rich, very well preserved shells in life position. Beds sit conformably on each other and there is no evidence for discontinuities. Lithologies do not vary much and are mostly composed of alternating clays, silts and muds of grey, green and dark colours, and sand of yellowish, cream and greyish colours. Black peats and lignites are sporadically found, never exceeding one meter in thickness, mostly of a few centimetres. Very thin (ca. 10 cm) reddish paleosoils and (ca. 20-40 cm) dark green biomicrite are also seen; the latter could be thicker (up to 3 metres) as most of them are recorded below and above coring gaps. The bottom parts of the core associated with the Ramón Formation are similar in composition, but thicker beds of white/cream sand seem to prevail towards the base of the section.

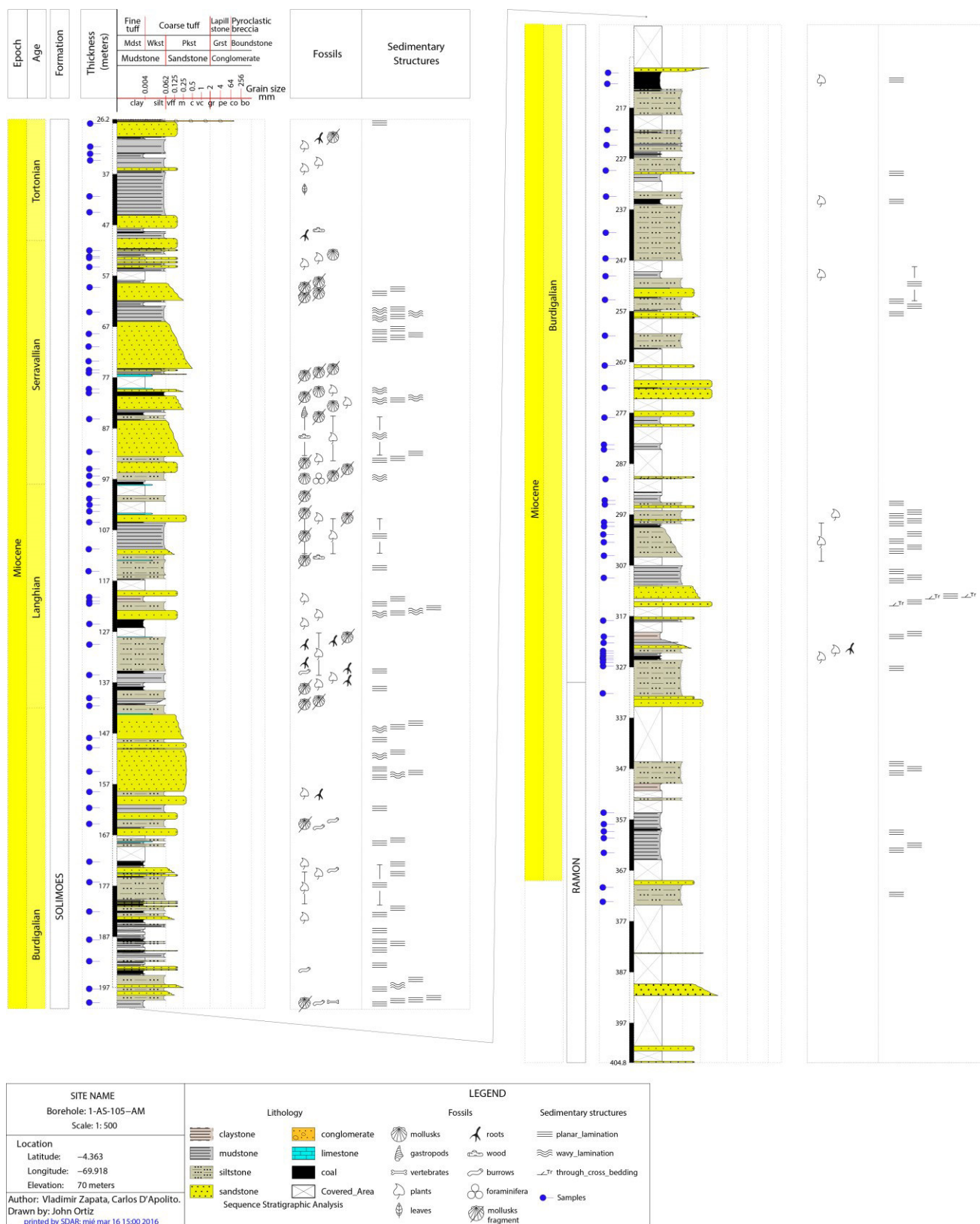


Figure 2.1. Summary stratigraphic log of well 1-AS-105-AM (for a more detailed version see Appendix

Fig. 9.4). Age/Stages are from current thesis (Chapter 5).

## **Chapter 3: General Methods**

### **3.1 Introduction**

This section presents all methods used in each of the following chapters, from sample collection and lab techniques to analytical/statistical approaches. Details on the sequence stratigraphy analysis are not included here as this was not performed by me, but it can be found in the appendix material at the end of this thesis.

### **3.2 Sampling**

In March and April 2012 I visited the facilities of CPRM in Manaus together with a sedimentologist for core descriptions and sample collection. We were granted a permit to collect a quarter of the circumference (ca. 1 to 2 cm<sup>3</sup>) of the core and selected fine and organic rich sediments that were appropriate for palynological study. Sampling was undertaken throughout the entire core 1-AS 105-AM. The sampling strategy collected one sample at every meter, unless there was a lithological change, in which case sampling resolution was increased to guarantee all lithologies were sampled, especially at lithological boundaries. This in turn meant collecting sometimes many samples per meter. This strategy follows from previous studies of colleagues who found weak signals of marine incursions in other cores of the area (e.g. rare dinoflagellate cysts or foraminiferal linings), we assumed a priori that the incursions were rather rapid and hence even a small sampling gap could mean we would completely miss a marine incursion. Samples were given individual field collection numbers and later they were incorporated into the Smithsonian Tropical Research Institute online geological database at <http://biogeodb.stri.si.edu/jaramillo2/fossildb/> that generates labels and numbers that were used for laboratory analytical purposes. Well preserved gastropod and bivalve shells were collected as well.

### 3.3 Laboratory processing

Pollen samples were processed following conventional methods (Wood *et al.* 1996). They consist of digestion of ca. 10 grams of sediment in hydrochloridric acid for 12 hours (for carbonate extraction), then digestion in hydrofluoric acid for at least 24 hours (for silicate extraction). Neutralisation with water and decanting were used after each acid digestion step. The dissolved mineral portion was later sieved in 250 µm and 10 µm meshes for elimination of coarser portions. The fraction <10 µm was then disaggregated in ultrasonic bath and the less dense organic matter portion recovered. This residue was cleaned in ultrasonic bath for a few seconds and concentrated in a centrifuge. Slides were then mounted with polyvinyl alcohol and sealed with Canada balsam. Analyses were done on an optical microscope Zeiss Axioskop 40 and photomicrographs taken in 1000 x magnification with a Canon EOS-500D. Multiple pictures were made in different focus for each species. Afterwards, when possible, pictures were stacked up together using Adobe Photoshop in order to include as much focus as possible to individual pictures. Laboratory processing was done by Paleoflora Ltda., Colombia, and pollen analyses performed by me at the University of Birmingham, UK.

Pollen counts were taken on every slide aiming for a minimum of 300 individual specimens of pollen plus spores. Reworked pollen and spores and other structures were also counted (dinocysts, algae cells, foraminiferal linings), but kept outside the 300 count. This results in the total count varying from sample to sample. Identification of pollen and spores followed local and regional publications that describe and illustrate the palynology of upper Tertiary deposits (Germeraad *et al.* 1968, Lorente 1986, Muller *et al.* 1987, Hoorn 1993, Silva-Caminha *et al.* 2010) and the online electronic morphological database of Jaramillo and Rueda (2013) accessible at <http://biogeodb.stri.si.edu/jaramillo/palynomorph/pollen> that hosts updated taxonomic information of northern south America pollen and spores publications of



Cretaceous and Cenozoic ages. Dinoflagellate cyst identifications were supported by the help of Neogene specialist Stephen Louwye (University of Ghent, Belgium).

### 3.4. Palynostratigraphy

The age of core 105-AM was determined almost entirely by means of palynology using the method of Graphic Correlation (Shaw 1964, Edwards 1984, 1989). Events of first (FAD) and last (LAD) appearance of the studied section were imported to the software GraphCor (Hood 1998) where the analyses were run. Topmost and bottommost samples were ignored in order to minimize the edge effect (Foote 2000) that artificially increases the numbers of FADs at the bottom and LADs at the top of sections. Next, a correlation was performed between the composite standard section of Jaramillo *et al.* (2011) and core 105-AM. The composite section of Jaramillo *et al.* (2011) was created from 70 sections of late Cretaceous to Recent ages in the Colombian Llanos, Andean foothills and western Venezuela, this zonation was erected using Graphic Correlation and Constrained Optimization (Kemple *et al.* 1995) and calibrated against the geological timescale (Gradstein *et al.* 2012) using data on foraminifera, magnetostratigraphy and bulk carbon isotopes ( $\delta^{13}\text{C}_{\text{TOM}}$ ). The zonation is currently the most updated one in northern South America and has very good correlation with older zonations from Venezuela (Germeraad *et al.* 1968, Muller *et al.* 1987). Because the composite units are calibrated, ages can be derived for all events of FAD and LAD and therefore ages for individual samples can be interpolated. Recently, some new sections have been added to the composite, which increased the number of taxa used for correlation. One section in particular was key for the correlations made in this thesis: the borehole Saltarin in the Colombian Llanos (Fig. 1.1) is a ca. 700 m Miocene section with very good pollen recovery and displayed a better correlation to the initial composite section than did 105-AM. After addition of Saltarin to the composite, more events could be used to

correlate the resulting composite to 105-AM. These events are marine surfaces (dinocysts acmes) and Sequence Stratigraphical points from the correlation between 105-AM and Saltarin, and altogether they refine the age model. Sequence Stratigraphy was performed by German Bayona (Jaramillo *et al.* in prep). A direct correlation between Saltarin and 105-AM was also performed aiming for similar results. After a careful investigation of suitable taxa to be used, the line of correlation (LOC) was traced manually in every round of correlation. The taxa used were chosen because they fall in the criteria of (i) having a frequent occurrence after their FAD, (ii) having a distinguished morphology that does not allow misidentification and (iii) having a well-known coverage and distribution in the previous zonations, what actually characterizes them as key taxa (see chapter 5 and Fig. 5.1). Correlation equations were then used to derive composite units, which in turn were transformed into ages. All lists of FAD and LAD events, equations for LOCs and R functions used to derive composite units and ages are shown in the Appendix (9.1.a-f).

Molluscan biostratigraphy was also explored as a dating tool. This could only be used for a short part of the section (from 52.9 to 83 m), where well preserved shells were found. Mollusc identification was supported by Frank Wesselingh, Naturalis Institute, Leiden, The Netherlands, and the results compared to the Amazon Molluscan zonation (Wesselingh *et al.* 2006a).

### **3.5. Palaeoecology**

In order to reconstruct the environmental settings in which the Solimões Formation was deposited, palynomorphs were grouped according to their environmental affinities: land pollen (pollen + spores), fresh water algae (*Botryococcus* spp + *Pediastrum* spp) and marine (dinocysts + foraminiferal linings). Among land pollen, subgroups were also adopted, like for instance the mangrove *Rhizophora* spp. (fossil type *Zonocostites* spp) and *Pelliciera* spp.

(fossil type *Lanagiopollis crassa*), palm trees, herbs, aquatic plants and others. A list with all known botanical affinities can be found in Appendix Table 9.2. These groups and subgroups were transformed into relative abundances of the total counts. Pollen diagrams were plotted with R package ‘rioja’ (Juggins 2015).

Floristic patterns were assessed in different manners. First, pollen diversity (here used as the total number of species) was estimated within-samples using rarefaction (Sanders 1968). This technique standardizes the sample size to a count number lower than the actual sample size. Such a procedure is necessary because the total number of species in a given sample is controlled by the numbers of specimens counted, which in turn vary from sample to sample. A cut-off number ( $n=226$ ) was chosen in order to maximize the number of samples to be included in the analysis, so samples with less than this value were not included in the diversity analysis. The diversity described above is a within-sample estimate, but groups of samples (among-sample) were also analysed once they were detected, i.e. when a set of samples has similar diversity estimates to another set of samples above or below. This was done with bootstrapped species accumulation curves (Gilinsky 1991). All analyses were performed in R package ‘vegan’ (Oksanen *et al.* 2015). A comparison with late Holocene pollen diversity was also attempted. Data from four Holocene cores in western Amazonia was sourced from the Latin American Pollen Database (Flantua *et al.* 2015). These sites were: Monica 1 (7,260 yrs Before Present (BP)), Monica 2 (4,010 yrs BP ) and Monica 3 (3,200 yrs BP) (Behling *et al.* 1999), which are located at the low terraces of the Caquetá River, approximately 460 km from core 1-AS-105-AM; and Quebrada del Amor (ca. 300 yrs) (Berrio *et al.* 2003), also located at the terraces of the Caquetá River, approximately 490 km from core 1-AS-105-AM. They were chosen because they are lowland sites in western Amazonia, other lowland sites in other areas or upland (montane) sites were not included as they could represent a particular vegetation type only (e.g. montane or submontane biomes),

or be too far away from the study site and therefore suffer influences of different biomes/plant diversity trends. Samples of these cores were combined into one dataset and subjected to the same analysis as Miocene samples.

Second, a multivariate approach was taken to explore the existence of palynofloristic gradients over time. If the abundance data of one species is one variable to be looked at among all samples, then there are as many variables as there are species, which in pollen studies tallies to the hundreds and makes it impractical for single species analysis. Instead, multivariate statistics compress all variables into a few axes of variation. These axes represent similarity showing how samples relate to each other (Legendre and Legendre 1998, Borcard *et al.* 2011) and can be used to explore patterns of the entire plant community on a given gradient that in this case is time. Two ordinations were used: Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA). Both techniques are rather similar, but CCA allows the addition of environmental variables (Ter Braak 1986), which in the present study was presence or absence of a given paleoenvironmental type (fresh or marine water). This was done to explore how much floristic change can be associated with particular environmental characteristic, i.e. inundations. DCA and CCA were performed in R package ‘vegan’ (Oksanen *et al.* 2015).

Third, standing diversity, originations and extinctions were calculated. These were used to show if diversity and community behaviours relate to times of specific high/low originations and extinctions. Originations and extinctions are simply the total number of species appearing for the first time or disappearing from the data set. Standing diversity is a more realistic estimate as it assumes a range-through approach of the data (Boltovskoy 1998). However, we cannot rely entirely on the standing diversity measures as it is heavily influenced by the edge effect (Foote 2000). A tentative method for estimating the edge effect was introduced by Jaramillo (2002, 2008). It consists of performing a piecewise regression on

both LAD and FAD data separately. Piecewise regressions fit two segmented regression lines to the data, choosing the lines with lowest residual. The breakpoint is the intersection between both lines, and can be interpreted as the stratigraphical point where the edge effect is minimal. Analyses of origination, extinction and standing diversity were run in R package ‘stratigraph’ (Green 2015). An R code for the piecewise regression was written by Jaramillo (2008) and is shown in the Appendix, adapted to the present data.

Finally, evolutionary models were used to test if there is a preferential direction in diversity change through time (Hunt 2006, 2008, Hunt and Carrano 2010). These models were originally created to fit models of body-size and other morphometric data, but they have been successfully used for diversity metrics (e.g. Sessa *et al.* 2012). The models tested were generalized random walk (GRW), unbiased random walk (URW) and stasis, and they were fitted to diversity estimates and ecological ordination scores. GRW assumes variation of the mean with a trended direction over time. URW and stasis are models that express no trend in the data, the difference is that in stasis there is no accumulation of change over time, and hence time is not significant, whereas in the URW there is variation over time but still no directionality is assumed. Bins of 0.5 Ma were used and model fit was compared using the corrected Akaike information criterion (AICc). Analyses were run in R package ‘paleoTS’ (Hunt 2015).

## Chapter 4. Systematic palynology

### 4.1. Introduction

In this section the palynology of core 1-AS-105-AM is described and illustrated. Descriptions are given to new forms of particular interest (either common and frequent stratigraphically or, if rare, with a characteristic morphology). Formal established species from the literature are illustrated but not described. A number of new combinations are proposed for species placed in invalid genera. Descriptions of new species were ordered by major morphological groups (e.g. Monoletes, Triletes, Monocolpate, etc), then alphabetical within section. New species and genera were erected and compared to existing species in the literature using the online morphological database of Jaramillo and Rueda (2013), which hosts updated taxonomic information on pollen and spores of Cretaceous-Cenozoic ages in northern South America, including key Amazon sites where a high number of species have been described and identified in this study. In total, 491 different palynomorph types were recognized, of which 320 are pollen and 82 are spores species. Newly described species are 76 pollen (38 genera, of which two are proposed as new) and 25 spores (17 genera); fourteen pollen species are new combinations. The terminology used in descriptions follows Punt *et al.* (2007), with some modifications from Jaramillo and Dilcher (2001). All grains are located using the England Finder coordinate system (EF).

For spores the following terminology is used:

- 1) TLI refers to the Trilete index, which is 'radius length/ (spore diameter/2)';
- 2) MLI refers to the Monolete index, which is 'laesura length/spore length'.

For pollen the terms used are:

- 1) CPi is calculated in equatorial view, being 'colpi length/polar diameter';
- 2) CEi was calculated in polar view, being 'colpi length/equatorial diameter'.

## 4.2. Pteridophyte and bryophyte spores (alphabetical order)

### Monolete spores

Genus *Echinosporis* Krutzsch 1967

**Type species.** *Echinosporis echinatus* Krutzsch 1967

*Echinosporis densiechinatus* sp. nov.

Plate 1, figures 1-4

**Holotype.** Plate 1, figures 1-2, sample 22140, EF P-40-1/2

**Paratype.** Plate 1, figures 3-4, sample 22326, EF V-37

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, oval; monolete, curvature absent, laesura mid-sized, 15  $\mu\text{m}$ , MLI 0.6, margo absent, commissure indistinct, intexine 1-2  $\mu\text{m}$ , echinate.

Echinae densely and evenly distributed over the entire surface of the spore, conical shaped, 2-3  $\mu\text{m}$  tall, 1-1.5  $\mu\text{m}$  wide at base and 1-2  $\mu\text{m}$  spaced.

**Dimensions.** Equatorial diameter 15-(17.6)-18  $\mu\text{m}$ ; polar diameter 26-(25.3)-25  $\mu\text{m}$ ; polar/equatorial 1.43. nm=3, no=14.

**Remarks.** *Echinosporis* sp. Raine 1981 has shorter and sparser echinae. *Polypodiisporites echinatus* Jaramillo and Dilcher 2001 has much longer and wider conical spines and is less dense.

**Derivation of name.** After the dense echinate pattern.

Genus *Laevigatosporites* Raine 1981

**Type species.** *Laevigatosporites vulgaris* Ibrahim, 1933

*Laevigatosporites caoticus* sp. nov.

Plate 1, figures 5-6

**Holotype.** Plate 1, figures 5, sample 22287, EF H-5-1/2

**Paratype.** Plate 1, figures 6, sample 22272, EF J-11

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, reniform; monolete, curvature absent, laesura mid-sized, 20  $\mu\text{m}$ , MLI 0.5, margo indistinct, commissure indistinct, intexine 1  $\mu\text{m}$ , scabrate. Scabrae densely and evenly distributed over the entire surface of the spore, short < 0.5  $\mu\text{m}$ , and sometimes anastomosing creating small rugulae.

**Dimensions.** Equatorial diameter 27  $\mu\text{m}$ ; polar diameter 40  $\mu\text{m}$ ; polar/equatorial 1.48  $\mu\text{m}$ ; nm=2, no=55.

**Remarks.** *Punctatosporites* sp. A Brenner and Bickoff 1992 is smaller and scabration is almost indistinct meanwhile in *L. caoticus* sp. nov. it is dense and readily recognizable. *P. scabratus* (Couper 1958) Singh 1971 is granulate-scabrate.

**Derivation of name.** After the irregular (chaotic) scabrate surface.

*Laevigatosporites cultellus* sp. nov.

Plate 1, figures 7-8

**Holotype.** Plate 1, figures 7, sample 22279, EF K-24

**Paratype.** Plate 1, figures 8, sample 22158, EF K-6-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, reniform; monolete, curvature absent, laesura long, 58  $\mu\text{m}$ , MLI 0.78, margo raised as a blade along the entire laesura, 6-4  $\mu\text{m}$  wide, commissure straight, intexine 1-1.5  $\mu\text{m}$ , laevigate.

**Dimensions.** Equatorial diameter 46  $\mu\text{m}$ ; polar diameter 74-(65)-56  $\mu\text{m}$ ; polar/equatorial 1.41; nm=2, no=2.



**Remarks.** *Laevigatosporites belfordii* Burger 1976 differs from *L. cultellus* sp. nov. in having a depression in the laesura area.

**Derivation of name.** After the blade-like margo, the Latin word ‘cultellus’ means dagger.

**Genus** *Microfoveolatosporis* Krutzsch 1959

**Type species.** *Microfoveolatosporis pseudodentatus* Krutzsch 1959

*Microfoveolatosporis simplex* sp. nov.

Plate 1, figures 11

*Microfoveolatosporis* sp.1 Silva-Caminha *et al.* 2010

**Holotype.** Plate 1, figures 11, sample 22354, EF Q-26-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, reniform; monolete, curvature absent, laesura distinct, middle small, 15 µm, MLI 0.36, margo distinct, 2 µm wide, segmented to granulate, commissure distinct, straight, intexine 1 µm. Foveolate. Foveolae circular to elongate, 0.7-1.5 µm wide, 1.2 µm apart. Homobrochate, uniformly distributed over the entire surface of the spore.

**Dimensions.** Equatorial diameter 26 µm; polar diameter 41 µm; equatorial/polar diameter 1.57; nm=1, no=1.

**Remarks.** *M. skottsbergii* (Selling, 1946) Srivastava, 1971 is larger and has larger foveolae.

**Derivation of name.** After the rather simple morphology.

**Genus** *Polypodiisporites* Potonié 1956

**Type species.** *Polypodiisporites favus* Potonié 1956

*Polypodiisporites densus* sp. nov.

Plate 1, figures 13-14

**Holotype.** Plate 1, figures 13, sample 22277, EF D-45-4

**Holotype.** Plate 1, figures 14, sample 22158, EF W-9-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, oval; monolete, curvature absent, laesura mid-sized, 20  $\mu\text{m}$ , MLI 0.47, margo indistinct, commissure indistinct, intexine 2  $\mu\text{m}$ , verrucate. Verrucae densely and evenly distributed over the entire surface of the spore, closely spaced and of constant height, 1  $\mu\text{m}$  tall, 1-4  $\mu\text{m}$  wide and 1  $\mu\text{m}$  spaced.

**Dimensions.** Equatorial diameter 35-(29.5)-24  $\mu\text{m}$ ; polar diameter 42-(46)-50  $\mu\text{m}$ ; polar/equatorial 1.55; nm=2, no=8.

**Remarks.** *Polypodiisporites* aff. *speciosus* Sah 1967 is laevigate on the proximal face and has larger irregular verrucae with bases that sometimes connect. This is not a feature in *P. densus*. A thicker sporoderm and laevigate proximal side is a feature of *P. pachyexinatus*. Conversely *P. usmensis* (Van der Hammen, 1956a) Khan and Martin 1972 is gemmate while *P.? planus* Silva-Caminha *et al.* 2010 has flat verrucae. The uniform size and distribution of verrucae is characteristic of *P. densus* sp. nov.

**Derivation of name.** After the dense verrucate pattern.

*Polypodiisporites discretus* sp. nov.

Plate 2, figures 1-2

**Holotype.** Plate 2, figures 1, sample 22140, EF N-5-2/4

**Paratype.** Plate 2, figures 2, sample 22140, EF G-23-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, reniform; monolete, curvature absent, laesura mid-sized, 20 $\mu\text{m}$ , MLI 0.52, margo indistinct, commissure indistinct, intexine 1  $\mu\text{m}$ ,

verrucate. Verrucae sparsely distributed over the entire surface of the spore, very short, <0.5  $\mu\text{m}$  tall, 2  $\mu\text{m}$  wide and 3-5  $\mu\text{m}$  apart.

**Dimensions.** Equatorial diameter 25-(25.5)-26  $\mu\text{m}$ ; polar diameter 38  $\mu\text{m}$ ; polar/equatorial 1.49  $\mu\text{m}$ ; nm=2, no=68.

**Remarks.** *Polypodiisporites* aff. *specious* Sah 1967 is laevigate on the proximal face and has larger irregular verrucae. *P. scabraproximatus* Silva-Caminha *et al.* 2010 has a scabrate proximal face.

**Derivation of name.** After the discrete verrucate pattern.

*Polypodiisporites fossulatus* sp. nov.

Plate 2, figures 3-4

**Holotype.** Plate 2, figures 3-4, sample 22418, EF V-43-1/3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, reniform; monolete, curvature absent, laesura mid-sized, 13  $\mu\text{m}$ , MLI 0.54, margo absent, commissure indistinct, intexine 1.5  $\mu\text{m}$ , foveo-fossulate. Foveolae and fossulae irregularly distributed over the surface of the spore, foveolae appearing isolated less often than anastomosed, in which case they create fossulae. Fossulae of variable size and distribution, sometimes seen as long ridges, very short, <0.5  $\mu\text{m}$  tall, 0.5-1  $\mu\text{m}$  wide and 1-1.5  $\mu\text{m}$  apart. Where fossulae are wider, small verrucae or granulae can be present.

**Dimensions.** Equatorial diameter 15  $\mu\text{m}$ ; polar diameter 24  $\mu\text{m}$ ; polar/equatorial 1.6  $\mu\text{m}$ . nm=1, no=5.

**Remarks.** No fossulate monoletes have been recorded yet. *Microfoveolatosporis* Krutzsch 1959 species are foveolate.

**Derivation of name.** After the fossulate pattern.

**Genus** *Punctatosporites* Ibrahim 1933

**Type species.** *Punctatosporites minutus* Ibrahim 1933

*Punctatosporites? latrubessei* sp. nov.

Plate 2, figures 9-12

**Holotype.** Plate 2, figures 9-10, sample 22354, EF J-19

**Paratype.** Plate 2, figures 11-12, sample 22402, EF E-11-3/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial; monolete, reniform, curvature absent, laesura mid-sized, 18  $\mu\text{m}$ , MLI 0.58, simple, commissure distinct, invaginated, ends pointed; intexine 1  $\mu\text{m}$ . Scabrate. Scabrae very densely and evenly distributed over the entire surface of the spore, forming a mat-like layer, 1.5-2  $\mu\text{m}$  tall.

**Dimensions.** Equatorial diameter 18-(18.5)-19  $\mu\text{m}$ ; polar diameter 31-(31.5)-32  $\mu\text{m}$ ; polar/equatorial 1.7  $\mu\text{m}$ . nm=2, no=4.

**Remarks.** *Punctatosporites minutus* Ibrahim 1933, *P. scabratus* (Couper 1958) Singh 1971, *P. walkomii* de Jersey 1962 and *Laevigatosporites granulatus* Jaramillo *et al.* 2007 have considerably less dense scabrae and thinner intexine.

**Derivation of name.** After the geologist Edgardo Latrubesse.

**Genus** *Reticulosporis* Krtuzsch 1959

**Type species.** *Reticulosporis miocenicus* (Selling) Krutzsch 1959

*Reticulosporis diversus* sp. nov.

Plate 2, figures 13-16

**Holotype.** Plate 2, figures 13-14, sample 22354, EF G-7

**Paratype.** Plate 2, figures 15-16, sample 22354, EF T-13

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, reniform; monolete, curvature absent, laesura distinct, straight, 20 µm long, tapering, margo distinct, 1.5 µm wide, also tapering, commissure distinct, intexine 1-2 µm. Reticulate. Very few lumina, very broad and of irregular shape, curvy and sometimes lobed. Lumina 10-20 µm wide, muri 1 µm thick, lumina 2 µm apart. Occasionally, luminae are thin, having a canaliculated appearance. Intrareticulate surface laevigate to sparsely granulose, with circular granules, 1-2 µm wide.

**Dimensions.** Equatorial diameter 21-(23)-25 µm; polar diameter 36-(38)-40 µm; polar/equatorial 1.65; nm=2, no=2.

**Remarks.** All other monolete-reticulate spores have more regular reticulate patterns.

**Derivation of name.** After its different (from the Latin “diversus”) morphology.

### Trilete spores

**Genus** *Camarozonosporites* Pant ex Potonié 1956, emend. Klaus 1960

**Type species.** *Camarozonosporites cretaceous* (Weyland and Krieger 1953) Potonié 1956

*Camarozonosporites fossulatus* sp. nov

Plate 3, figures 4-5

**Holotype.** Plate 3, figures 4-5, sample 22277, EF S-39

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, circular to subcircular; trilete, curvatura absent, laesura distinct, straight, radii middle sized, 8 µm, TLI 0.61, margo distinct, very thin, 0.5-1 µm wide, commissure distinct, straight, ends pointed; interradian crassitude, intexine 3 µm at the interradian area and 1 µm at corners. Fossulate over the entire surface of the spore. Fossulae long, curvey and irregular, 1 µm wide, 2-3 µm apart, sometimes bifurcating.

**Dimensions.** Equatorial diameter length 26  $\mu\text{m}$ ; equatorial diameter width 25  $\mu\text{m}$ , length/width 1.04; nm=1, no=1.

**Remarks.** *Camarozonosporites* Pant ex Potonié 1956, emend. Klaus 1960 accommodates verrucate spores with interrarial crassitude. *C. crassus* Silva-Caminha *et al.* 2010 is verrucate. *Camarozonosporites* sp. 1 Jaramillo and Dilcher 2001 has thinner interrarial crassitude, is laevigate proximally and fossulae is smaller.

**Derivation of name.** After lobate appearance of the interrarial crassitude.

**Genus** *Camarozonosporites* Pant ex Potonié 1956, emend. Klaus 1960

**Type species.** *Camarozonosporites cretaceous* (Weyland and Krieger 1953) Potonié 1956

*Camarozonosporites trilobatus* sp. nov

Plate 3, figures 6-9

**Holotype.** Plate 3, figures 6-7, sample 22277, EF U-35-4

**Holotype.** Plate 3, figures 8-9, sample 22278, EF H-37-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, straight, radii middle sized, 10  $\mu\text{m}$ , TLI 0.83, margo distinct, very thin, 0.5-1  $\mu\text{m}$  wide, commissure distinct, straight, intexine 5-6  $\mu\text{m}$  at interrarial area and 1  $\mu\text{m}$  at corners. Verrucate. Verrucae distributed on the entire surface of the spore. Verrucae larger and irregular on the distal face, and smaller and circular on the proximal face. Verrucae distally can be very large and irregular. Around the equator, verrucae merge and form interrarial crassitude that can sometimes resemble lobes. Verrucae 2-7  $\mu\text{m}$  wide, 2-5  $\mu\text{m}$  tall, 1-4  $\mu\text{m}$  apart.

**Dimensions.** Equatorial diameter length 24-(24.5)-25  $\mu\text{m}$ ; equatorial diameter width 20-(20.5)-22  $\mu\text{m}$ , length/width 1.19, nm=2, no=2.

**Remarks.** *Camarozonosporites* Pant ex Potonié 1956, emend. Klaus 1960 accommodates verrucate spores with interrarial crassitude. *C. crassus* Silva-Caminha *et al.* 2010 has smaller and more regular verrucae and thinner interrarial crassitude.

**Derivation of name.** After lobate appearance of the interrarial crassitude.

**Genus** *Cicatricosisporites* Potonié and Gelletich, 1933 emend. Potonié, 1966

**Type species.** *Cicatricosisporites dorogensis* Potonié and Gelletich, 1933

*Cicatricosisporites pseudograndiosus* sp. nov.

Plate 3, figures 12-13

**Holotype.** Plate 3, figures 12-13, sample 22278, EF H-8-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, straight, radii long reaching equator, 40µm, TLI 1, margo indistinct, commissure distinct, straight; intexine 0.7 µm. Cicatricose over the entire surface of the spore. Distal ribs 5-7 µm wide, flat, straight, separated by thin grooves 1 µm wide. Ribs arranged in one set on the distal face, running parallel to the equator, sometimes bifurcating, ribs extremities pinch out gently toward the equator and coalesce in the apices. On the proximal face, ribs are similar to the distal face but run in three set, one in each interrarial area.

**Dimensions.** Equatorial diameter length 51-(63)-75 µm; equatorial diameter width 45-(52.5)-60 µm, length/width 1.2; nm=2, no=4.

**Remarks.** *Cicatricosisporites subrotundus* Brenner 1963 has ribs arranged parallel to the equator in the distal face. *C. pseudograndiosus* sp. nov. differs from *M. grandiosus* (Kedves and Sole de Porta, 1963) Dueñas, 1980 and other species of *Cicatricosisporites* in having much larger ribs and a much higher ribs-groove width ratio.

**Derivation of name.** After resemblance with *Magnastriatites grandiosus* (Kedves and Sole de Porta, 1963) Dueñas, 1980.

**Genus** *Cingulatisporites* Thomson in Thomson and Pflug, 1953

**Type species.** *Cingulatisporites levispeciosus* Pflug, 1953, in Thomson and Pflug, 1953

*Cingulatisporites cristatus* sp. nov.

Plate 3, figures 14

**Holotype.** Plate 3, figures 14, sample 22279, EF U-43

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, circular to triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, curvey, radii long, 10 µm, reaching equator, TLI 0.9, margo distinct, very thin <0.5 µm wide, commissure indistinct, intexine 1 µm. Laevigate with sporadic small verrucae on the surface of the spore. Cingulum is cristate, 2-5 µm thick. Cingulum sculptural elements 1 µm wide, 1 µm tall.

**Dimensions.** Equatorial diameter length 22-(22.5)-23 µm; equatorial diameter width 20-(20.5)-21 µm, length/width 1.09; nm=2, no=2.

**Remarks.** Thickness of the cingulum can vary but there is not a clear interradian crassitude. Other species of *Cingulatisporites* do not present a cristate cingulum.

**Derivation of name.** After cristate cingulum.

*Cingulatisporites matisiense* sp. nov.

Plate 3, figures 15-18

**Holotype.** Plate 3, figures 15-16, sample 22278, EF S-19

**Paratype.** Plate 3, figures 17-18, sample 22278, EF E-12-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.



**Description.** Spores single, symmetry radial, circular, cingulate; trilete, curvatura imperfecta, laesura distinct, straight, radii long, reaching equator, 12 µm long, TLI 0.8, margo distinct, 2 µm wide, serrulate border, commissure distinct, straight, cingulum 2-3 µm. Verrucate-rugulate. Verrucae sparse and tend to be clustered in the proximal face, circular, 1-2 µm wide. Distal face has sparse and irregular rugulae, 4-6 µm wide, 2-3 µm thick.

**Dimensions.** Equatorial diameter length 30-(32.5)-35 µm; equatorial diameter width 30 µm; length/width 1.08; nm=2, no=2.

**Remarks.** *Cingulatisporites verrucatus* Regali *et al.* 1974 has a much wider cingulum and laevigate proximal face. *Polypodiaceoisporites pseudopsilatus* Lorente 1986 has a triangular prominence on the distal face. *Pteridaceoisporis gemmatus* Silva-Caminha *et al.* 2010 has thicker cingulum, shorter radii and denser and more diverse verruca-rugulae.

*Cingulatisporites rugulatus* Silva-Caminha *et al.* 2010 has waving commissure, thinner margo, proximal rugulae and distal scabrae.

**Derivation of name.** After the amazon indigenous tribe Matis.

### **Genus** *Echinatisporis* Krutzsch 1959

**Type species.** *Echinatisporis longechinus* Krutzsch 1959

*Echinatisporis connectus* sp. nov.

Plate 4, figures 7-10

**Holotype.** Plate 4, figures 7-8, sample 22278, EF P-24

**Paratype.** Plate 4, figures 9-10, sample 22140, EF L-13

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, circular; trilete, curvatura absent, laesura distinct, irregular, radii reaches the equator, 20 µm long, TLI 0.8, marginate, margo 1 µm wide, commissure irregular; intexine 2-3 µm. Echinulate. Spines present on the entire surface,

but more densely distributed on the distal face; 2 µm wide at base, 2 µm tall, conical shapes, closely spaced, 1-2 µm apart. Spines tend to connect to another spine and sometimes create rugulae.

**Dimensions.** Equatorial diameter length 50-(51)-52 µm; equatorial diameter width 46-(48)-50 µm, length/width 1.06 µm; nm=2, no=2.

**Remarks.** *E. brevispinosus* Jaramillo, Dilcher 2001 and *E. muelleri* (Regali *et al.*, 1974) Silva-Caminha *et al.* 2010 and *E. circularis* Silva-Caminha *et al.* 2010 are much smaller and differ in spine morphology.

**Derivation of name.** After connection between spines.

*Echinatisporis infantus* sp. nov.

Plate 4, figures 11-13

**Holotype.** Plate 4, figures 11-12, sample 22140, EF S-51-2

**Paratype.** Plate 4, figures 13, sample 22170, EF F-32-2/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, circular; trilete, curvatura absent, laesura distinct, straight, radii middle-sized, 10 µm long, TLI 0.66, marginate, margo very thin, 0.7 µm wide, commissure straight; intexine 0.5 µm. Echinulate. Spines present on the entire surface; 0.5 µm wide at base, 1 µm tall, 2-3 µm apart. Spines small, conical, evenly distributed.

**Dimensions.** Equatorial diameter length 30 µm; equatorial diameter width 26 µm, length/width 1.15; nm=1, no=2.

**Remarks.** *Planisporites* sp. 2 Jaramillo and Dilcher has larger spines and margo is raised. *Acantotriletes levidensis* Balme 1957 has larger spines and radii that reaches equator, *E. circularis* Silva-Caminha *et al.* 2010 is thicker and has larger spines.

**Derivation of name.** After the reduced size of spines.

**Genus** *Hamulatisporis* Krutzsch 1959

**Type species.** *Hamulatisporis caperatus* (van Hoeken-Klinkenberg, 1964) Schrank 1994

*Hamulatisporis bare* sp. nov.

Plate 5, figures 4-5

**Holotype.** Plate 5, figures 4-5, sample 22140, EF V-9-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, circular to triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, straight, radii middle sized, 15 µm long, TLI 0.75, margo thin, 1 µm wide, commissure distinct, straight; intexine 1-2 µm. Hamulate over the entire surface of the spore, slightly coarser distally. Rugula 1 µm wide, curvey, mostly connected and sometimes forming isolated foveolae. Fossula 1.5 µm wide.

**Dimensions.** Equatorial diameter length 36-(38)-40 µm; equatorial diameter width 33-(35)-37 µm, length/width 1.08 µm, nm=2, no=2.

**Remarks.** *H. caperatus* (Van Hoeken-Klinkenberg 1964) Schrank 1994 has a finer hamulate pattern. *H. insignis* (Norris 1967) Kedves 1995 has interrarial crassitude, rugulae have a radial arrangement and amb is more circular.

**Derivation of name.** After the Amazon indigenous group Baré.

**Genus** *Ischyosporites* Balme 1957

**Type species.** *Ischyosporites crateris* Balme 1957

*Ischyosporites dubius* sp. nov.

Plate 5, figures 8-11

**Holotype.** Plate 5, figures 8-9, sample 22140, EF Q-6-1

**Paratype.** Plate 5, figures 10-11, sample 22293, EF U-11

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, straight, radii mid-sized, 12  $\mu\text{m}$  long, TLI 0.52, marginate, margo 2-3  $\mu\text{m}$  wide, undulating to straight, thinning outwards, commissure distinct, straight; intexine 1.5  $\mu\text{m}$ . Verrucate. Verrucae present over the entire surface of the grain. Most verrucae anastomose to form a rugulate pattern; verrucae very variable, 5  $\mu\text{m}$  wide, 0.5-1  $\mu\text{m}$  tall, with fossulae separating them, of irregular shape.

**Dimensions.** Equatorial diameter length 27-(36.5)-46  $\mu\text{m}$ ; equatorial diameter width 21-(33)-45  $\mu\text{m}$ , length/width 1.1; nm=2, no=7.

**Remarks.** *I. problematicus* Jaramillo and Dilcher 2001 is fossulate, with higher proportion of fossula in comparison to sculptural elements (verrucae, rugulae). *I. variegatus* (Couper 1958) Jansonius and Hills 1990 is distally foveo-reticulate and proximally granulose to verrucose. *I. badagriensis* Jan du Chene *et al.* 1978 has broad reticulum. *I. crateris* Balme 1957 is thicker and foveolate. *I. dubius* sp. nov. has also a resemblance with *Verrucatotriletes* spp., the difference being the anastomosing character of verrucae and the present of fossula.

**Derivation of name.** After the large variation of sculptural elements.

*Ischyosporites granulatus* sp. nov.

Plate 5, figures 12-13

**Holotype.** Plate 5, figures 12-13, sample 22293, EF D-5-1/2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, triangular to triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, straight, radii long, almost reaching the equator, 14  $\mu\text{m}$  long, TLI 0.73, marginate, margo thick, 3-2  $\mu\text{m}$ , with an irregular outer border, commissure

distinct, straight; intexine 3-2  $\mu\text{m}$ . Rugulate distally and granular to verrucate proximally.

Rugulae irregular, long and bifurcating, connecting to each other, sometimes forming sporadic luminae, and of constant width; 4-5  $\mu\text{m}$  wide and of variable length. Granules on the proximal face are sparse, circular and 1-3  $\mu\text{m}$  wide.

**Dimensions.** Equatorial diameter length 29-(33.5)-38  $\mu\text{m}$ , equatorial diameter width 26-(31)-36  $\mu\text{m}$ , length/width 1.08; nm=2, no=2.

**Remarks.** Other species of *Ischyosporites* are fossulate and reticulate. Rugulae in *I. granulatus* sp. nov. do not form regular luminae.

**Derivation of name.** After granulate ornamentation.

### **Genus** *Lycopodiumsporites* Thiergart 1938

**Type species.** *Lycopodiumsporites agathoecus* (Potonié) Thiergart 1938

*Lycopodiumsporites clavatooides* sp. nov.

Plate 5, figures 15-16

**Holotype.** Plate 5, figures 15-16, sample 22279, EF T-16

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, triangular-obtuse-convex; trilete, curvatura absent, laesura distinct, straight, radii middle sized, 12 $\mu\text{m}$  long, TLI 0.8, margo indistinct, commissure indistinct; intexine 3-4  $\mu\text{m}$ . Reticulate over the entire surface of the spore.

Lumina circular, 2-3  $\mu\text{m}$  wide, thin muri, 0.7  $\mu\text{m}$  wide. Muri very tall, 3  $\mu\text{m}$  tall.

**Dimensions.** Equatorial diameter length 30-(34.5)-39  $\mu\text{m}$ ; equatorial diameter width 29-(34)-36  $\mu\text{m}$ , length/width 1.01; nm=2, no=2.

**Remarks.** *L. novomexicanum* Drugg 1967 and *Retitriletes austraclavatooides* (Cookson 1953) Döring *et al.* in Krutzsch 1963 have shorter muri and larger luminae. *Retitriletes altimuratus* Silva-Caminha *et al.* 2010 has shorter muri and indistinct laesura. *Retitriletes baqueroense*

Archangelsky and Villar de Seoane 1998 and *L. fastigioides* (Couper 1953) Boltenhagen 1967 are laevigate on the proximal face.

**Derivation of name.** After the resemblance with spores of the modern species *Lycopodium clavatum*.

**Genus** *Neoraistrickia* (Cookson 1953) Potonié 1956

**Type species.** *Neoraistrickia truncata* (Cookson 1953) Potonié 1956

*Neoraistrickia dubiosa* sp. nov.

Plate 6, figures 2-5

**Holotype.** Plate 6, figures 2-3, sample 22293, EF K-50-1/2

**Paratype.** Plate 6, figures 4-5, sample 22326, EF J-14

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, circular; trilete, curvatura absent, laesura distinct, irregular to straight, radii short, 8 µm long, TLI 0.66, marginate, margo very thin < 1 µm wide, commissure distinct; intexine 1-1.5 µm. Baculate. Bacula present on the entire surface of the spore; 1-1.5 µm wide at base, 1.5-3 µm tall, 1 µm apart, densely distributed and most are constricted at the base.

**Dimensions.** Equatorial diameter length 24-(24.5)-25 µm; equatorial diameter width 22-(23)-24 µm, length/width 1.06; nm=2, no=3.

**Remarks.** *N. truncata* (Cookson 1953) Potonié 1956 has larger, less dense bacula and shape is more triangular.

**Derivation of name.** After the dubious variation of the ornamentation elements, constricted and non-constricted.

**Genus** *Psilatriletes* Van der Hammen 1954 ex Potonié 1956

**Type species.** *Psilatriletes detortus* (Weyland and Krieger 1953) Potonié 1956

*Psilatriletes delicatus* sp. nov.

Plate 6, figures 10-11

**Holotype.** Plate 6, figures 10, sample 22257, EF P-39-2

**Paratype.** Plate 6, figures 11, sample 22148, EF M-6-3/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, circular; trilete, curvatura absent, laesura distinct, radii long almost reaching the equator, 10 µm long, TLI 0.69, slightly marginate, margo 0.5 µm wide, commissure straight, ends pointed; intexine 0.7 µm. Laevigate. Spore very easily folded, especially around the equator, often creating a false cingulate appearance.

**Dimensions.** Equatorial diameter length 22-(25.5)-29 µm, equatorial diameter width 19-(22)-25 µm, length/width 1.15; nm=2, no=8.

**Remarks.** *Cyathidites minor* Couper 1953 and *C. australis* Couper 1953 are triangular-subtriangular and with thicker intexine. *Biretisporites potoniaei* Delacourt and Sprumont 1955 has radii reaching the equator and thicker intexine and margo. *Hydrosporites minor* Silva-Caminha *et al.* 2010 is smaller and thicker (1.5 µm).

**Derivation of name.** After the thin and foldable intexine.

*Psilatriletes marginata* sp. nov.

Plate 6, figures 13-15

**Holotype.** Plate 6, figures 13-14, sample 22277, EF D-50-2

**Paratype.** Plate 6, figures 15, sample 22277, EF H-25-3/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, triangular-obtuse-straight to slightly convex; trilete, curvatura absent, laesura distinct, straight, radii medium-sized, 10µm long, TLI 0.76, marginate, margo 3-4 µm wide, wider toward the centre the Y-mark, commissure straight, ends pointed; intexine 1.5-2 µm. Laevigate to micropitted. Sporoderm is very often densely perforated but laevigate specimens have been seen. Margo is characteristic, it can be straight or deflected at the central area of the spore, forming two segments.

**Dimensions.** Equatorial diameter length 26-(31.5)-37 µm; equatorial diameter width 25-(28.5)-32 µm; length/width 1.1; nm=2, no=12.

**Remarks.** *Dictyophyllidites impensus* (Heldlund 1966) Singh 1983 is circular and has thinner margo. *Hydrosporites minor* Silva-Caminha *et al.* 2010 is smaller, more circular and has thinner margo with granulae.

**Derivation of name.** After the presence of a margo.

#### **Genus** *Rotverrusporites* Döring 1964

**Type species.** *Rotverrusporites obscurilaesuratus* (Pocock 1962) Döring 1964

*Rotverrusporites amazonicus* sp. nov.

Plate 7, figures 5-8

**Holotype.** Plate 7, figures 5-6, sample 22277, EF E-49-1

**Paratype.** Plate 7, figures 7-8, sample 22279, EF G-8-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, circular to subcircular; trilete, curvatura absent, laesura distinct, straight, radii long, 12µm long, almost reaching equator, TLI 0.80, margo distinct, 1 µm wide, straight, commissure distinct, straight; intexine 2 µm thick. Verrucate over the entire surface of the spore. Verrucae 0.5-2 µm wide, 1 µm tall, circular, 0.5 µm apart. Wider verrucae (2 µm wide) are more predominant than smaller ones.



**Dimensions.** Equatorial diameter length 30-(33)-36  $\mu\text{m}$ ; equatorial diameter width 30-(33)-36  $\mu\text{m}$ , length/width 1; nm=2, no=2.

**Remarks.** *Rotverrusporites rupununiensis* van der Hammen and Burger 1966 is larger, much thicker and has larger verrucae. *Rotverrusporites obscurilaesuratus* (Pocock 1962) Doring 1964 does not have distinct laesura.

**Derivation of name.** After the Amazon.

*Verrucatotriletes pseudoviruleoides* sp. nov.

Plate 7, figures 11-12

**Holotype.** Plate 7, figures 11-12, sample 22278, EF O-9-3/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Spores single, symmetry radial, circular to subcircular; trilete, curvatura absent, laesura distinct, radii middle sized, 17  $\mu\text{m}$  long, TLI 0.73, margo absent, commissure distinct, straight, intexine 2  $\mu\text{m}$ . Verrucate. Verrucate sparse, veru short, over the entire spore.

Verrucae 1  $\mu\text{m}$  wide, < 0.5  $\mu\text{m}$  tall, circular, irregularly distributed over entire grain, 2  $\mu\text{m}$  apart.

**Dimensions.** Equatorial diameter length 46  $\mu\text{m}$ ; equatorial diameter width 44  $\mu\text{m}$ , length/width 1.04; nm=1, no=2.

**Remarks.** *V. viruleoides* Jaramillo *et al.* 2007 has smaller and denser verrucae and thinner intexine.

**Derivation of name.** After similarity to *V. viruleoides* Jaramillo *et al.* 2007.

### 4.3. Anteturma Pollenites (ordered by morphological groups, then alphabetical)

#### Inaperturate

**Genus** *Inaperturopollenites* (Pflug) Potonié 1958

**Type species** *Inaperturopollenites dubius* (Potonié & Venitz) Thomson & Pflug 1953

*Inaperturopollenites tectatus* sp. nov.

Plate 8, figures 4

**Holotype.** Plate 8, figures 4, sample 22278, EF T-50

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, amb circular, inaperturate. Tectate, exine 1  $\mu\text{m}$ , nexine 0.3  $\mu\text{m}$ , columellae distinct, 0.3  $\mu\text{m}$ , tectum 0.3  $\mu\text{m}$  thick, micropitted, pits < 0.5  $\mu\text{m}$ , circular, homobrochate.

**Dimensions.** Polar diameter 24  $\mu\text{m}$ , nm=1, no=21.

**Remarks.** Usually appears folded. *Inaperturopollenites cursis* Sarmiento, 1992 and *I.*

*curvimuratus* Regali 1974 are reticulate; *I. dubius* (Potonié and Venitz) Pflug and Thomson 1953 in Thomson and Pflug 1953 and *I. simplex* Regali 1974 are atectate-psilate;

**Derivation of name.** After tectate exine.

#### Monosulcate

**Genus** *Arecipites* Wodehouse 1933 emend. Nichols *et al.* 1973

**Type species** *Arecipites punctatus* Wodehouse, 1933 ex Potonié, 1958

*Arecipites membranousus* sp. nov.

Plate 8, figures 10

**Holotype.** Plate 8, figures 10, sample 22460, EF P-20-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, bilateral, heteropolar, prolate to perprolate. Monocolpate, colpi long, reaching poles, ends rounded, borders straight, slightly tapered, colpi 36  $\mu\text{m}$  long, CPI 0.92. Colpi marginate, margo 1  $\mu\text{m}$  wide with a membranous extension reaching halfway through the equatorial diameter in each side of the colpus, membrane very thin, <0.5  $\mu\text{m}$  thick, irregular border and tapering; tectate, exine 1.5  $\mu\text{m}$ , nexine 0.5  $\mu\text{m}$ , columellae 0.5  $\mu\text{m}$ , distinct and packed, tectum 0.5  $\mu\text{m}$ , thick; micropitted, pits <0.5  $\mu\text{m}$ , circular, homobrochate, densely distributed.

**Dimensions.** Polar diameter 35-(37)-39  $\mu\text{m}$ , equatorial diameter 18-(18.5)-19  $\mu\text{m}$ , polar/equatorial 2; nm=2, no=2.

**Remarks.** Monocolpate pollen with this type of margo have not been described in Tertiary deposits of northern South America. *Arecipites regio* (Van der Hammen and Garcia, 1966) Jaramillo and Dilcher, 2001 is similar but has a different, often indistinct margo.

**Derivation of name.** After the membranous appearance of the margo.

**Genus** *Longapertites* van Hoeken-Klinkenberg 1964

**Type species** *Longapertites marginatus* van Hoeken-Klinkenberg 1964

*Longapertites lisus* sp. nov.

Plate 8, figures 15-16

**Holotype.** Plate 8, figures 15, sample 22279, EF T-9-1/3

**Paratype.** Plate 8, figures 16, sample 22418, EF G-20-1/2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, bilateral, isopolar, prolate. Zonosulcate, grain nearly split in two halves; tectate, exine 1  $\mu\text{m}$ , nexine 0.4  $\mu\text{m}$ , columellae 0.3  $\mu\text{m}$ , distinct and packed, tectum 0.4  $\mu\text{m}$ , thick; psilate to very finely micropitted. Columellae tips can be seen through tectum.

**Dimensions.** Polar diameter 42-(44)-46  $\mu\text{m}$ , equatorial diameter 26-(27)-28  $\mu\text{m}$ , polar/equatorial 1.62; nm=2, nm=2.

**Remarks.** Other *Longapertites* species are micropitted and reticulate.

**Derivation of name.** After the smooth surface of the grain.

*Longapertites utilis* sp. nov.

Plate 9, figures 1-2

**Holotype.** Plate 9, figures 1-2, sample 22272, EF K-6-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, bilateral, isopolar, perprolate. Monocolpate, colpi longer than the length of grain, almost splitting the grain in two and thus one polar area is open, ends open, borders straight, colpi 34  $\mu\text{m}$  long (on each side), CPi 0.94. Colpi marginate, margo 1  $\mu\text{m}$  wide; tectate, exine 1  $\mu\text{m}$ , nexine 0.4  $\mu\text{m}$ , columellae 0.2  $\mu\text{m}$ , indistinct, tectum 0.4  $\mu\text{m}$ , thick; micropitted, lumina <0.5  $\mu\text{m}$ , elongate, homobrochate, densely distributed, very shallow, lumina sometimes anastomosing and forming fossulae..

**Dimensions.** Polar diameter 36  $\mu\text{m}$ , equatorial diameter 18  $\mu\text{m}$ , polar/equatorial 2; nm=1, no=2.

**Remarks.** *Longapertites fossuloides* Gonzalez 1967 has much wider and deeper fossulae and is bigger. *L. marginatus* van Joeken-Klinkenberg 1964 is larger and has heterobrochate micropitted ornamentation. *L. microfoveolatus* Adegoke and Jan du Chene 1978 has a different outline shape (elliptical) and shorter colpus. *L. vaneendenburgi* Germeraad *et al.* 1968 is much larger and evenly micropitted.

**Derivation of name.** After its subtle appearance.

**Genus** *Retimonocolpites* Pierce 1961

**Type species** *Retimonocolpites dividiuus* Pierce 1961

*Retimonocolpites normalis* sp. nov.

Plate 9, figures 11-12

**Holotype.** Plate 9, figures 11-12, sample 22402, EF U-37-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, bilateral, isopolar, prolate spheroidal. Monocolpate, colpus long, reaching poles, ends open, borders straight, colpi 26  $\mu\text{m}$  long, 3-4  $\mu\text{m}$  wide, simple, CPi 1. Semitectate, exine 1.5  $\mu\text{m}$ , nexine 0.5  $\mu\text{m}$ , columellae 0.5  $\mu\text{m}$ , distinct, ca. 0.5  $\mu\text{m}$  apart, tectum 0.5  $\mu\text{m}$  thick; reticulate, lumina <0.5  $\mu\text{m}$ , circular to slightly elongate, homobrochate, muri 0.5  $\mu\text{m}$  wide

**Dimensions.** Polar diameter 26  $\mu\text{m}$ , equatorial diameter 24  $\mu\text{m}$ , polar/equatorial 1.08; nm=1, no=1.

**Remarks.** Similar to *R. claris* Sarmiento 1992 but *R. normalis* nov. sp. differs in having clearly distinct columellae and homobrochate reticulum meanwhile *R. claris* has indistinct columellae, is sometimes intectate, and has quite variable lumina size. *R. longicolpatus* Lorente 1986 is micropitted to finely reticulate. *R. absyae* Hoorn 1993 is heteropolar and has a shorter colpus.

**Derivation of name.** After the rather generalised morphology.

**Zonosulcate**

**Genus** *Proxapertites* Van der Hammen 1956

**Type species** *Proxapertites operculatus* Van der Hammen 1956

*Proxapertites finus* sp. nov.

Plate 9, figures 13-14

**Holotype.** Plate 9, figures 13-14, sample 22326, EF M-21-1/3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, heteropolar, oval shaped. Zonosulcate, colpus long, splitting grain in two uneven halves (smaller=54 x 91  $\mu$ m, larger=65 x 91  $\mu$ m), borders straight, marginate, margo thin, 1  $\mu$ m long. Atectate, exine 2  $\mu$ m thick, covered by a thin and almost translucent perine, <0.5  $\mu$ m thick, that forms a very coarse reticulum, lumina ca. 10  $\mu$ m wide, very irregular, muri 1.5  $\mu$ m wide, somewhat curvilinear.

**Dimensions.** Wider diameter 84-(91)-98  $\mu$ m, smaller diameter 58-(65)-72  $\mu$ m, nm=2, no=8.

**Remarks.** Halves usually found isolated; reticulum variable in size, sometimes not seen.

**Derivation of name.** After the fine perine layer.

**Trichotomosulcate**

**Genus** *Trichotomosulcites* Couper 1953

**Type species** *Trichotomosulcites subgranulatus* Couper 1953

*Trichotomosulcites amazonicus* sp. nov.

Plate 9, figures 17

**Holotype.** Plate 9, figures 17, sample 22140, EF D-32-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, heteropolar, triangular-obtuse-straight to slightly concave.

Trichotomosulcate, colpus long, radii 19  $\mu$ m, reaching equator, ends usually open to rounded, marginate, margo 1  $\mu$ m wide. Semitectate, exine 1.5  $\mu$ m, exine 0.5  $\mu$ m, columellae 0.5  $\mu$ m, distinct, < 0.5  $\mu$ m apart, tectum 0.5  $\mu$ m thick. Microreticulate, homobrochate, lumina <0.5  $\mu$ m wide, circular, muri ca. 0.5  $\mu$ m wide.

**Dimensions.** Equatorial diameter length 26-(32)-38  $\mu\text{m}$ , equatorial diameter width 26-(32)-38, length/width 1; nm=2, no=10.

**Remarks.** *Trichotomosulcites ornatus* Boltenhagen 1976 has much wider reticulum; *T. laevigatus* Boltenhagen 1976 is psilate.

**Derivation of name.** After the Amazon.

*Trichotomosulcites normalis* sp. nov.

Plate 9, figures 18

**Holotype.** Plate 9, figures 18, sample 22405, EF Q-42-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, heteropolar, triangular-obtuse-convex. Trichotomosulcate, colpus long, radii 14  $\mu\text{m}$  long, 3-4  $\mu\text{m}$  wide, almost reaching equator, ends rounded, marginate, margo restricted to middle section of the sulcus, ca. 1  $\mu\text{m}$  wide and pinching out towards colpi ends. Tectate, exine 2.1  $\mu\text{m}$ , exine 0.7  $\mu\text{m}$ , columellae 0.7  $\mu\text{m}$ , distinct, dense (but not packed) and very thin, tectum 0.7  $\mu\text{m}$  thick. Psilate, columellae tips seen through tectum, giving a micropitted appearance.

**Dimensions.** Equatorial diameter length 37-(38)-39  $\mu\text{m}$ , equatorial diameter width 35-(36.5)-38, length/width 1.04; nm=2, no=3.

**Remarks.** *Trichotomosulcites laevigatus* Boltenhagen 1976 has a narrower colpus with wide margo and seems to be atectate.

**Derivation of name.** After the rather simple morphology.

## Monoporate

**Genus** *Monoporopollenites* (Meyer 1956) Potonié 1960

**Type species** *Monoporopollenites gramineoides* Meyer

*Monoporopollenites annuloides* sp. nov.

Plate 10, figures 2-3

**Holotype.** Plate 10, figures 1-2, sample 22140, EF F-36

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, bilateral, isopolar, circular. Monoporate, pore 3.5-5  $\mu\text{m}$  wide, annulate, annulus 1.5-2  $\mu\text{m}$ . Tectate, exine 1  $\mu\text{m}$ , nexine 0.4  $\mu\text{m}$ , columellae 0.2  $\mu\text{m}$ , indistinct, tectum 0.3  $\mu\text{m}$ . Psilate to finely micropitted, pits < 0.5  $\mu\text{m}$  wide, circular, scattered over entire grain.

**Dimensions.** 22-(22.5)-23  $\mu\text{m}$  across; nm=2, no=49.

**Remarks.** Differs from *Monoporopollenites annulatus* (Van der Hammen, 1954) Jaramillo and Dilcher, 2001 in being thicker, having pitted ornamentation and wider pore and annulus.

**Derivation of name.** After its resemblance with *M. annulatus*.

## Dicolpate

**Genus** *Dicolpopollis* Pflanzl 1956, emend Potonié

**Type species** *Dicolpopollis kockeli* Pflanzl 1965

*Dicolpopollis? costatus* sp. nov.

Plate 10, figures 4-5

**Holotype.** Plate 10, figures 3-4, sample 22460, EF D-48-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, amb sub-circular. Dicolporate, ectocolpi short, ends rounded, 12  $\mu\text{m}$  long, costate, costa produced by a thickening of the whole exine around colpi, 2  $\mu\text{m}$  thick, 8  $\mu\text{m}$  wide, endopores, pore characteristics not visible. Atectate, exine 1-2  $\mu\text{m}$  thick, psilate.



**Dimensions.** Equatorial diameter length 22-(24.6)-26  $\mu\text{m}$ , equatorial diameter width 21-(22.6)-25  $\mu\text{m}$ , length/width 1.08; nm=3, no=2.

**Remarks.** The genus *Dicolporites* van der Hammen 1956 is *nomen nudum*. *Dicolpopollis* Pflanzl 1956 accommodates dicolpate grains; I place the present fossil type provisionally in the genus *Dicolpopollis*. *D.? costatus* could be related to the modern genus *Macoubea* (Apocynaceae) which is tricolporate and dicolporate (Colinvaux *et al.* 1999).

**Derivation of name.** After costate aperture.

**Botanical affinity.** *Macoubea* (Apocynaceae).

### Tricolpate

#### Genus *Foveotricolpites* Pierce 1961

**Type species** *Foveotricolpites sphaeroides* Pierce 1961

*Foveotricolpites colpiconstrictus* Hoorn 1994 nov. comb.

**Basionym.** *Retitricolpites colpiconstrictus* Hoorn 1994, page 38, plate 4, fig. 2.

**Specimens.** Plate 10, figures 17-18, sample 22140, EF T-9-1

**Description.** Monad, radial, isopolar, prolate; tricolpate, endo and ectocolpi coinciding, long, 22  $\mu\text{m}$  long, CPI 0.73, marginate, margo 1  $\mu\text{m}$  thick, ends pointed, constriction present at mesocolpia area of colpi; polar area small, 10  $\mu\text{m}$  wide; tectate, exine 2  $\mu\text{m}$  thick, slightly thicker at apocolpia, nexine 0.5  $\mu\text{m}$  thick, columellae 0.5  $\mu\text{m}$  thick, packed, tectum 1  $\mu\text{m}$  thick; micropitted, pits 0.5  $\mu\text{m}$ , 0.5  $\mu\text{m}$  apart, evenly and densely distributed over the entire grain.

**Dimensions.** Polar diameter 30  $\mu\text{m}$ , equatorial diameter 22  $\mu\text{m}$ , polar/equatorial 1.36; nm=1, no=10.

**Remarks.** *Psilatricolporites* van der Hammen 1956b ex Pierce 1961 is an obligate later synonym of *Tricolporites* van der Hammen 1954 (non Erdtman 1949) because they have the same type species; as *Tricolpites* is not validly published and a later synonym of *Clethra*, so is *Psilatricolporites* (Jansonius and Hills 1976, card 2234). *Foveotricolpites* Pierce 1961 accommodates subprolate tricolpate pollen with foveolate ornamentation.

*Foveotricolpites simplex* Gonzalez 1967 nov. comb.

**Basionym.** *Retitricolpites simplex* Gonzalez 1967, page 31, plate 2, fig. 1.

**Specimens.** Plate 11, figures 1-2, sample 22418, EF X-17

**Specimens.** Plate 11, figures 3, sample 22436, EF L-10-1/2

**Description.** Monad, radial, isopolar, prolate; tricolp(or)ate, endo and ectocolpi coinciding, 32 µm long, very slightly marginate, margo 0.5 µm wide, CEi 0.68, CPi 0.78, borders straight, ends pointed, polar area very small, 6 µm wide; endopores circular, simple, 10 µm wide; tectate, exine 2.5 µm thick, nexine 0.7 µm thick, columellae 1 µm thick, 0.5 µm wide, 0.5 µm apart, tectum 0.7 µm thick, perforated; foveolate to microreticulate appearance, lumina 0.5 µm wide, muri 0.5 µm thick, densely and evenly distributed over the entire grain.

**Dimensions.** Equatorial view: polar diameter 36-(38.5)-41 µm, equatorial diameter 20-(24)-28, polar/equatorial 1.60. Polar view: polar diameter length 41 µm, polar diameter width 41 µm, length/width 1; nm=3, no=216.

**Remarks.** *Retitricolpites* Van der Hammen 1956 ex Pierce 1961 is invalid and a later synonym of *Neea* (Jansonius and Hills 1976, card 2401). *Foveotricolpites* Pierce 1961 accommodates subprolate tricolpate pollen with foveolate ornamentation.

**Genus** *Ladakhipollenites* Mathur and Jain 1980

**Type species** *Ladakhipollenites levis* (Sah and Dutta 1966) Mathur and Jain 1980

*Ladakhipollenites baitacolumellatus* sp. nov.

**Holotype.** Plate 11, figures 4-5, sample 22257, EF K-45-3

**Paratype.** Plate 11, figures 6, sample 22140, EF D-16-1/2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate to subprolate, amb circular; tricolpate, colpi 16  $\mu\text{m}$  long, CEi 0.47, CPi 0.58, long, borders very slightly invaginating, ends rounded, ectocolpi marginate, margo 5  $\mu\text{m}$  wide and 1  $\mu\text{m}$  thick, formed by the decrease of columellae thickness towards colpi, also slightly costate, costa 1  $\mu\text{m}$  wide; polar area small, 6  $\mu\text{m}$  wide; tectate, exine 2  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, columellae 1  $\mu\text{m}$  thick, columellae thin, 0.5  $\mu\text{m}$  wide, 0.5  $\mu\text{m}$  apart, tectum 0.5  $\mu\text{m}$  thick; tips of columellae seen through tectum, giving a foveolate appearance. Psilate.

**Dimensions.** Equatorial view: Polar diameter 34  $\mu\text{m}$ , equatorial diameter 25-(27)-29  $\mu\text{m}$ , polar/equatorial 1.25. Polar view: equatorial diameter length 32  $\mu\text{m}$ , equatorial diameter width 32, length/width 1; nm=3, no=7.

**Remarks.** *Psilatricolpites acerbus* Gonzalez 1967 has packed columellae. *P. anconis* Hoorn 1993 has indistinct columellae and is smaller. *P. clarissimus* (van der Hammen, 1954) van der Hammen and Wymstra 1964 has a different type of margin. *P. colpiconstrictus* van Hoeken-Klinkenberg 1966 has constriction of the colpi. *P. polaroides* Gonzalez 1967 has thicker exine at poles. *P. hammenii* Boltenhagen 1976 is atectate.

**Derivation of name.** After the Portuguese word ‘baita’, meaning big, many or good in reference to the columellae that are very clearly visible.

*Ladakhipollenites colpiconstrictus* van Hoeken-Klinkenberg 1966 nov. comb.

**Basionym:** *Psilatricolpites colpiconstrictus* van Hoeken-Klinkenberg 1966, page 41, plate 1, fig. 13.

**Specimens.** Plate 11, figures 7-8, sample 22445, EF U-35

**Description.** Monad, radial, isopolar, prolate-spheroidal; tricolpate, endo and ectocolpi coinciding, 18  $\mu\text{m}$  long, CPi 0.66, borders straight, ends rounded, polar area small, 5  $\mu\text{m}$  wide, costate, costa 1  $\mu\text{m}$  wide; constriction present at mesocolpia area of colpi; tectate, exine 2  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, columellae 1  $\mu\text{m}$  thick, distinct, 0.3  $\mu\text{m}$  wide, 0.2  $\mu\text{m}$  apart, tectum 0.5  $\mu\text{m}$  thick; tips of columellae seen through tectum. Psilate.

**Dimensions.** Polar diameter 27  $\mu\text{m}$ , equatorial diameter 25  $\mu\text{m}$ , polar/equatorial 1.08; nm=1, no=10.

**Remarks.** *Psilatricolporites* van der Hammen 1956b ex Pierce 1961 is an obligate later synonym of *Tricolporites* van der Hammen 1954 (non Erdtman 1949) because they have the same type species; as *Tricolpites* is not validly published and a later synonym of *Clethra*, so is *Psilatricolporites* (Jansonius and Hills 1976, card 2234). *Ladakhipollenites* Mathur and Jain 1980 accommodates tricolpate psilate pollen grains.

*Ladakhipollenites nanus* sp. nov.

Plate 11, figures 9-10

**Holotype.** Plate 11, figures 9-10, sample 22148, EF G-12

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate to perprolate; tricolpate, colpi 18-15  $\mu\text{m}$  long, CPi 0.81-0.78, borders straight, ends pointed, simple, polar area small, 5  $\mu\text{m}$  wide; tectate, exine 1  $\mu\text{m}$  thick, nexine 0.3  $\mu\text{m}$  thick, columellae 0.5  $\mu\text{m}$  thick, indistinct, tectum 0.3  $\mu\text{m}$  thick. Psilate.

**Dimensions.** Polar diameter 19-(19.5)-20  $\mu\text{m}$ , equatorial diameter 9-(10.5)-12  $\mu\text{m}$ , polar/equatorial 1.85; nm=2, no=7.

**Remarks.** *Psilatricolpites minutus* Gonzalez 1967 has constriction in the mesocolpi, appearing tricolporate.

**Derivation of name.** After the small size.

*Ladakhipollenites simplissimus* sp. nov.

Plate 11, figures 11-12

**Holotype.** Plate 11, figures 11-12, sample 22282, EF R-11-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, amb circular; tricolpate, endo and ectocolpi coinciding, 20 µm long, CEi 0.8, long, borders slightly invaginated, ends pointed, margo 3 µm wide x 1 µm thick, formed by the decrease of columellae thickness towards colpi, polar area small, 6 µm wide; tectate, exine 1.8 µm thick, nexine 0.6 µm thick, columellae 0.6 µm thick, distinct, tectum 0.6 µm thick. Psilate. Columellae tips can be seen through tectum and sometimes are indistinct.

**Dimensions.** Equatorial diameter length 21-(24)-26 µm, equatorial diameter width 18-(22)-25 µm, length/width 1.09; nm=3, no=4.

**Remarks.** Similar to *L. baitacolumellatus* sp. nov., but differs in the fact that exine is thinner and columella are much thinner and appearing more discrete. *P. clarissimus* (van der Hammen, 1954) van der Hammen and Wymstra, 1964 has a different type of margin.

**Derivation of name.** After its rather simple morphology.

**Genus** *Retibrevitricolpites* Hoeken-Klinkenberg 1966

**Type species** *Retibrevitricolpites triangulatus* Hoeken-Klinkenberg 1966

*Retibrevitricolpites pseudoretibolus* sp. nov.

Plate 12, figures 1-2

**Synonymy.** *Retibrevitricolpites* sp. 1 Silva-Caminha *et al.* 2010 (?)

**Holotype.** Plate 12, figures 1, sample 22140, EF W-13-2

**Paratype.** Plate 12, figures 2, sample 22287, EF H-8-1/2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, amb circular; tricolpate, colpi simple, 4 µm long, CEi 0.18, short, borders straight, ends pointed, polar area large, 14µm wide; tectate, exine 1.8-2 µm thick, nexine 0.6 µm thick, columellae 0.6 µm thick, distinct, tectum 0.6 µm thick. Microreticulate. Lumina 0.5-1 µm, circular, muri 0.5-1 µm wide, homobrochate. Nexine endocracks can be seen in different degrees of intensity.

**Dimensions.** Equatorial diameter length 22-(25)-28 µm, equatorial diameter width 22-(24.75)-27.5 µm, length/width 1.01; nm=2, no=36.

**Remarks.** *Retibrevitricolpites retibolus* Leidekmeyer 1966 is tricolp(or)ate and has shorter colpi. *R. distinctus* van Hoeken-Klinkenberg 1966 has much larger heterobrochate reticulum. *R. triangulatus* van Hoeken-Klinkenberg 1966 and *R. deltoides* Dueñas 1986 have strong triangular amb.

**Derivation of name.** After its similarity with *R. retibolus*.

### **Genus** *Retitrescolpites* Sah 1967

**Type species** *Retitrescolpites typicus* Sah 1967

*Retitrescolpites brevicolpatus* sp. nov.

Plate 12, figure 3

**Holotype.** Plate 12, figure 3, sample 22506, EF R-5-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular amb; tricolpate, colpi 14 µm long, CEi 0.4, short, costate, borders straight, ends pointed, polar area 20µm wide, costa 2 µm wide, 2 µm

thick; semitectate, exine 2.5  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, columellae distinct, 1.5  $\mu\text{m}$  thick, 1  $\mu\text{m}$  wide, 1  $\mu\text{m}$  apart, tectum very thin, 0.5  $\mu\text{m}$  thick, almost not visible, giving the wall a retipilate appearance on cross section. Reticulate, lumina 3-4  $\mu\text{m}$  wide, curvimate to irregular, muri 1  $\mu\text{m}$  wide, simplicolumellate, homobrochate.

**Dimensions.** Polar diameter length 35-(37.3)-41  $\mu\text{m}$ , polar diameter width 27-(30)-33  $\mu\text{m}$ , length/width 1.24; nm=3, no=13.

**Remarks.** *Retitrescolpites* Sah 1967 accommodates retitricolp(or)ate with coarse retipilate or reticulate exine. Its type species, *R. typicus* Sah 1967 is described as having “muri usually sinuous”, in other words curvimate. *R. ? irregularis* (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001 is colporate and nexine is thicker than the sexine, the opposite of *R. brevicolpatus* sp. nov. *R. magnus* (Gonzalez, 1967) Jaramillo and Dilcher 2001 and *R. saturum* Jaramillo and Dilcher 2001 are longicolpate.

**Derivation of name.** After the short colpi.

### **Genus** *Rhoipites* Wodehouse 1933

**Type species** *Rhoipites bradleyi* Wodehouse 1933

*Rhoipites? colpiverrucosus* sp. nov.

Plate 12, figures 5-6

**Holotype.** Plate 12, figures 5-6, sample 22522, EF H-10-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, amb circular; tricolpate, colpi 28  $\mu\text{m}$  long, CEi 0.7, mid sized, borders straight, ends pointed, marginate, margo produced by a very slight decrease in columellae thickness towards colpi, 2  $\mu\text{m}$  wide, 1  $\mu\text{m}$  thick, costate, costa formed by small and irregular verrucae distributed along colpi, 1-2  $\mu\text{m}$  wide, polar 12  $\mu\text{m}$  wide; semitectate, exine 1  $\mu\text{m}$  thick, nexine 0.4  $\mu\text{m}$  thick, columellae 0.2  $\mu\text{m}$  thick, barely distinct, tectum 0.4

µm thick; stratification is not very clear, and the wall sometimes appears intectate.

Microreticulate, lumina 0.5 µm, circular to slightly elongate, 0.5 µm wide, muri 0.5 µm wide, homobrochate.

**Dimensions.** Equatorial diameter length 35-(37.5)-40 µm, equatorial diameter width 31-(32)-33 µm, Polar/equatorial diameter 1.17; nm=2, no=3.

**Remarks.** *Retitricolpites scabratus* Herngreen 1975 is thicker with margins that decrease in the size of pits towards the colpi and with a scabrate pattern along the colpi that decreases towards the polar area.

**Derivation of name.** After scabrae-verrucae along colpi.

*Rhoipites? pluricolumellatus* nov. sp.

Plate 12, figures 7-8

**Holotype.** Plate 12, figures 7-8, sample 22158, EF R-12-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, suboblate; tricolpate, colpi 11µm long, CPi 0.39, CEi 0.41 , mid-sized, borders straight, ends pointed, polar area 10 µm wide; semitectate, exine 1 µm thick, nexine 0.4 µm thick, columellae 0.2 µm thick, barely distinct, appears to be very thin and can often be seen through muri, tectum 0.4 µm thick. Reticulate, lumina 1-2 µm, circular to polygonal, muri 1 µm wide, pluricolumellate, homobrochate. A few lumina can be smaller, 1 µm wide, but these are not confined to any specific part of the grain's surface. In cross section, the tectum can be seen as an undulating feature, making the reticulum look more salient.

**Dimensions.** Equatorial view: polar diameter 28 µm, equatorial diameter 32 µm, polar/equatorial 0.87. Polar view: Equatorial diameter length 34 µm, equatorial diameter width 34 µm, length/width 1; nm=2, no=4.



**Remarks.** *Retitricolpites wijningae* Hoorn 1994 has much longer colpi and is prolate.

**Derivation of name.** After pluricolumellate pattern.

**Genus** *Bombacacidites* Couper 1960

**Type species** *Bombacacidites bombaxoides* Couper 1960

*Bombacacidites germeraadi* sp. nov.

Plate 13, figures 1-2

**Holotype.** Plate 13, figures 1-2, sample 22522, EF S-41-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, triangular-obtuse-straight grains. Tricolpate, planaperturate with colpi short, 18µm long and straight with pointed ends, CEi 0.45, costae 1.5 µm wide, 2 µm thick, costae surrounding the entire margin of the colpi, having a horse-shoe appearance, and slightly protruding, polar area large, 16 µm wide; semitectate, exine 2 µm thick, nexine 0.7 µm thick, columellae 0.6 µm thick, distinct, 0.5 µm wide, 0.5 µm apart, regularly distributed, tectum 0.7 µm thick. Microreticulate, lumina circular to slightly elongate, 0.5 µm wide, muri 0.5 µm wide, homobrochate.

**Dimensions.** Polar diameter length 40 µm, polar diameter width 33-(36.5)-40 µm, length/width 1.09; nm=2, no=16.

**Remarks.** *Bombacacidites soleaformis* Muller *et al.* 1987 is micropitted and has concave sides. *B. brevis* (Dueñas 1980) Muller *et al.* 1987 is smaller, has a circular to triangular-convex amb, thinner wall and costae (sometimes missing), and lacks bulging costae.

**Derivation of name.** After the palynologist J. H. Germeraad.

*Bombacacidites lorentae* Hoorn 1993 nov. comb.

**Basionym:** *Retitricolpites lorentae* Hoorn 1993, page 301, plate 1, fig. 27.

Plate 13, figures 3

**Specimens.** Plate 13, figures 3, sample 22140, EF P-11-3

**Description.** Monad, radial, isopolar, triangular-obtuse-concave; tricolporate, planaperturate, colpi medium, 18µm long, CEi 0.39, borders straight, rounded pointed, costae thin, 1 µm wide, 1 µm thick, polar area medium, 15 µm wide; semitectate, exine 2 µm thick, nexine 0.7 µm thick, columellae 0.7 µm thick, distinct, 0.7 µm apart, regularly distributed, tectum 0.7 µm thick. Reticulate, lumina circular to elongate, 1-0.5 µm wide, muri 1 µm wide, heterobrochate, lumina increases in size slightly (0.5 to 1 µm) towards polar ares, simplicolumellate.

**Dimensions.** Polar diameter length 46-(49)-52 µm, polar diameter width 43-(46)-49 µm, length/width 1.06; nm=2, no=9.

**Remarks.** *Retitricolpites* Van der Hammen 1956 ex Pierce 1961 is invalid and a later synonym of *Neea* (Jansonius and Hills 1976, card 2401). *Bombacacidites* Couper 1960 accommodates planaperturate pollen grains with affinity to genera of the Bombacoideae subfamily.

### Tricolporate

**Genus** *Echitricolporites* Van der Hammen 1956 ex Germeraad *et al.* 1968

**Type species** *Echitricolporites spinosus* Van der Hammen 1956 ex Germeraad *et al.* 1968

*Echitricolporites magnificus* sp. nov.

Plate 13, figures 7-10

*Malvacipolloides?* sp. 3 Silva-Caminha *et al.* 2010

**Holotype.** Plate 13, figures 7-8, sample 22365, EF S-9-2

**Paratype.** Plate 13, figures 9-10, sample 22279, EF D-10-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subprolate, circular amb; tricolporate, colpi mid-sized, 20  $\mu\text{m}$  long, borders slightly invaginated, ends pointed, CEi 0.57, costate, costa 1  $\mu\text{m}$  wide, 1  $\mu\text{m}$  thick, costae sometimes only in the central part of the colpi or completely absent, polar area 8  $\mu\text{m}$ ; endopores simple, characteristics not seen, sometimes not visible; tectate, exine 1.5  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, columellae 0.5  $\mu\text{m}$  thick, distinct, closely spaced, regularly distributed, tectum 0.5  $\mu\text{m}$  thick. Supratectal ornamentation echinate, echinae very small, < 0.5  $\mu\text{m}$  tall, 0.5  $\mu\text{m}$  wide at base, well-spaced and homogeneously distributed, 2  $\mu\text{m}$  apart. Intraechinae surface psilate to finely micropitted.

**Dimensions.** Polar diameter length 25-(30)-35  $\mu\text{m}$ , polar diameter width 25-(30)-35  $\mu\text{m}$ , length/width 1; nm=2, no=15.

**Remarks.** *Brevitricolpites microechinatus* Jaramillo and Dilcher 2001 is brevicolpate and intectate. *Echitricolpites communis* Regali *et al.* 1974 is colpate.

**Derivation of name.** After large size and clear morphology.

### **Genus** *Foveotricolporites* Pierce 1961

**Type species** *Foveotricolporites rhombohedralis* Pierce 1961

*Foveotricolporites lolongatis* sp. nov.

Plate 14, figures 2-3

**Holotype.** Plate 14, figures 2-3, sample 22290, EF R-37

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate-spheroidal; tricolporate, endocolpi long, 16  $\mu\text{m}$  long, very thin, almost inconspicuous, invaginating, ends pointed, CPi 0.84, simple; endopores simple, lolongate, 3 x 2  $\mu\text{m}$ ; tectate, exine 1  $\mu\text{m}$  thick, nexine 0.3  $\mu\text{m}$  thick, columellae 0.3  $\mu\text{m}$  thick, sometimes indistinct, tectum 0.3  $\mu\text{m}$  thick, overall stratification not

particularly clear. Ornamentation micropitted to psilate, pits circular,  $< 0.5\ \mu\text{m}$  wide,  $0.5\ \mu\text{m}$  apart. The endocolpi borders create a shadow in the pores that may look like an operculum.

**Dimensions.** Polar diameter 19-(19.6)-21  $\mu\text{m}$ , equatorial diameter 18-(18.6)-19  $\mu\text{m}$ , polar/equatorial 1.05; nm=3, no=102.

**Remarks.** Lolongate tricolporate pollen grains are not often described in northern South America. *Foveotricolporites rugulatus* and *F. sp. 3* Jaramillo and Dilcher 2001 are larger and coarsely ornamented. *Rhoipites guianensis* (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001 and *Retitricolporites ogowensis* Boltenhagen 1976 are reticulate.

**Derivation of name.** After lolongate pores.

#### **Genus** *Ladakhipollenites* Mathur and Jain 1980

**Type species** *Ladakhipollenites levis* (Sah and Dutta 1966) Mathur and Jain 1980

*Ladakhipollenites? cassioides* sp. nov.

Plate 14, figures 8-10

**Holotype.** Plate 14, figures 8, sample 22140, EF L-9

**Paratype.** Plate 14, figures 9-10, sample 22518, EF N-6-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate spheroidal; tricolporate, endo and ectocolpi coinciding, long, 19 $\mu\text{m}$  long, CPi 0.79, strongly constricted at equator, ends rounded, polar area 8  $\mu\text{m}$  wide, colpi costate, costae thin, 1  $\mu\text{m}$  wide, sometimes indistinct, pores characteristic not visible; tectate, exine 1.5  $\mu\text{m}$  thick, nexine 0.6  $\mu\text{m}$  thick, columellae 0.4  $\mu\text{m}$  long, sometimes indistinct, tectum 0.6  $\mu\text{m}$  thick; psilate. Sometimes wall structure can not be seen and seems to be atectate.

**Dimensions. Dimensions.** Polar diameter 24  $\mu\text{m}$ , equatorial diameter 21-(22.5)-24  $\mu\text{m}$ , polar/equatorial 1.06; nm=2, no=19.

**Remarks.** *Psilatricolporites costatus* Dueñas 1980 has much thicker costa. *P. vanus* Gonzalez 1967 is spherical, has nexine = sexine and colpi are simple (?). *L. constrictus* (van Hoeken-Klinkenberg 1966) nov. comb. is colpate, has thicker exine with columellae tips clearly visible through tectum.

**Derivation of name.** After resemblance with modern genus *Cassia* (Fabceae).

*Ladakhipollenites? corvattatus* sp. nov.

Plate 14, figures 11-12

**Holotype.** Plate 14, figures 11-12, sample 22278, EF H-11-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate spheroidal; tricolporate, ectocolpi mid-sized, 13 µm long, CPi 0.72, ends pointed, constricted at equator, costate, costae 1 µm wide, not extending until the end of colpi and gently fading away, giving the colpi the appearance of a bow tie, endopores very small and narrow, simple, lalongate, 2 x 0.5 µm wide. Polar area 7 µm wide; tectate, exine 1.5 µm thick, nexine 0.5 µm thick, columellae indistinct, 0.5 µm thick, tectum 0.5 µm thick; psilate.

**Dimensions.** Polar diameter 18-(19)-20 µm, equatorial diameter 16-(17)-18 µm, polar/equatorial 1.11; nm=2, no=2.

**Remarks.** *Psilatricolporites costatus* Dueñas 1980 has much thicker costa and longer colpi. *P. cassioides* nov. sp. has clear colpi constriction and costa along entire colpi. *Psilatricolpites constrictus* van Hoeken-Klinkenberg 1966 is colpate and has thicker exine.

**Derivation of name.** After the word *corvatta* meaning tie, for the appearance of the costa endocolpi.

*Ladakhipollenites? endoporatus* sp. nov.

Plate 14, figures 13-14

**Holotype.** Plate 14, figures 13-14, sample 22522, EF P-13-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate; tricolporate, ectocolpi long and very thin, 33 µm long, CP1 0.86, ends pointed, costate, costae 2 µm wide throughout entire extension, 1.5 µm thick near mesocolpia and decreasing to 1 µm thick towards apocolpia, borders straight, polar area small, 10 µm, endopores slightly lalongate, simple, 5 x 4 µm wide; tectate, exine 1.8 µm thick, nexine 0.5 µm thick, columellae packed, indistinct, 0.8 µm thick, tectum 0.5 µm thick; psilate.

**Dimensions.** Polar diameter 35-(36.5)-38 µm, equatorial diameter 22-(23.5)-25 µm, polar/equatorial 1.55; nm=2, no=11.

**Remarks.** *Ladakhipollenites? caribbiensis* (Muller *et al.*, 1987) Silva-Caminha *et al.* 2010 has simple colpi, much larger pores and thick, distinct columellae. *Psilatricolporites costatus* Dueñas 1980 has thicker costa and equatorial constriction. *P. atalayensis* Hoorn 1993 has perforated exine, equatorial constriction and larger pore. *P. crassoexinatus* Hoorn 1993 has thicker exine, with short columella and lalongate pores. *L.? magniporatus* (Hoorn 1993) nov. comb. has much wider pores and thicker tectum.

**Derivation of name.** After clear endopores.

*Ladakhipollenites? garzonii* Hoorn 1993 nov. comb.

**Basionym.** *Psilatricolporites garzonii* Hoorn 1993, page 304, plate 2, fig. 7-8.

Plate 14, figures 15-17

**Specimens.** Plate 14, figures 15-16, sample 22140, EF M-11-3/4

**Specimens.** Plate 14, figures 17 sample 22140, EF U-12

**Description.** Monad, radial, isopolar, pblate spheroidal, subtriangular amb; tricolporate, endocolpi short, 10  $\mu\text{m}$  long, costate, costae 1.5  $\mu\text{m}$  wide, 1.5  $\mu\text{m}$  thick, ectocolpi simple, very thin, borders slightly invaginated, ends pointed, polar area small, 7  $\mu\text{m}$ , CPi 0.71, CEi 0.71, endopores lalongate, simple, 2 x 1  $\mu\text{m}$  wide; tectate, exine 1.5  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$  thick, columellae distinct, 0.5  $\mu\text{m}$  thick, tectum 0.5  $\mu\text{m}$  thick; psilate to very finely micropitted. Thick exine in relation to small grain size.

**Dimensions.** Polar view: Equatorial diameter length 14  $\mu\text{m}$ , equatorial diameter width 14  $\mu\text{m}$ , length/width 1; Equatorial view: Polar diameter 14  $\mu\text{m}$ , equatorial diameter 15  $\mu\text{m}$ , polar/equatorial 0.93; nm=2, no=7.

**Remarks.** *Psilatricolporites* van der Hammen 1956b ex Pierce 1961 is an obligate later synonym of *Tricolporites* van der Hammen 1954 (non Erdtman 1949) because they have the same type species; as *Tricolpites* is not validly published and a later synonym of *Clethra*, so is *Psilatricolporites* (Jansonius and Hills 1976, card 2234). *Ladakhipollenites* Mathur and Jain 1980 accommodates tricolpate psilate pollen grains. The grain is provisionally placed in *Ladakhipollenites* as it cannot be satisfactorily placed in any other genus.

*Ladakhipollenites? labiatus* Hoorn 1993 nov. comb.

**Basionym.** *Psilatricolporites labiatus* Hoorn 1993, page 304, plate 2, fig. 14.

Plate 14, figures 18

**Specimens.** Plate 14, figures 18, sample 22140, EF L-16-4

**Description.** Monad, radial, isopolar, prolate; tricolporate, endo and ectocolpi coinciding, short and very thin, almost imperceptible, 12  $\mu\text{m}$  long, CPi 0.44, borders straight, ends pointed, costate, costae 5  $\mu\text{m}$  wide, restricted to area on top and bottom of pores, polar area broad, 12  $\mu\text{m}$ , endopores lalongate, simple, 5 x 2.5  $\mu\text{m}$  wide, pores areas protruding; atectate, exine 1  $\mu\text{m}$  thick; psilate.

**Dimensions.** Polar diameter 27  $\mu\text{m}$ , equatorial diameter 20  $\mu\text{m}$ , polar/equatorial 1.35; nm=1, no=1.

**Remarks.** *Psilatricolporites* van der Hammen 1956b ex Pierce 1961 is an obligate later synonym of *Tricolporites* van der Hammen 1954 (non Erdtman 1949) because they have the same type species; as *Tricolpites* is not validly published and a later synonym of *Clethra*, so is *Psilatricolporites* (Jansonius and Hills 1976, card 2234). *Ladakhipollenites* Mathur and Jain 1980 encompasses tricolpate psilate pollen grains. This pollen grain is placed provisionally in *Ladakhipollenites* as it cannot be satisfactorily placed in any other genus.

*Ladakhipollenites? magniporatus* Hoorn 1993 nov. comb.

**Basionym.** *Psilatricolporites magniporatus* Hoorn 1993, page 304, plate 2, fig. 24.

Plate 14, figures 19-20

**Specimen.** Plate 14, figures 19-20, sample 22336, EF E-43-4

**Description.** Monad, radial, isopolar, prolate; tricolporate, colpi long, 31  $\mu\text{m}$  long, CPi 0.88, endo and ectocolpi coinciding, simple, borders straight, costate, costae 2  $\mu\text{m}$  wide, 2  $\mu\text{m}$  thick, polar area 10  $\mu\text{m}$  wide, rounded, endopores simple, large, circular, 8 x 8  $\mu\text{m}$  wide, almost anastomosing each adjacent pores; tectate, thick exine, exine 2  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$  thick, columellae distinct, 0.5  $\mu\text{m}$  thick, tectum 0.5  $\mu\text{m}$  thick; psilate to microreticulate.

**Dimensions.** Polar diameter 35  $\mu\text{m}$ , equatorial diameter 20-(22)-24  $\mu\text{m}$ , polar/equatorial 1.59; nm=2, no=2.

**Remarks.** *Psilatricolporites* van der Hammen 1956b ex Pierce 1961 is an obligate later synonym of *Tricolporites* van der Hammen 1954 (non Erdtman 1949) because they have the same type species; as *Tricolpites* is not validly published and a later synonym of *Clethra*, so is *Psilatricolporites* (Jansonius and Hills 1976, card 2234). *Ladakhipollenites* Mathur and Jain 1980 embraces tricolpate psilate pollen grains. We place this pollen grain provisionally



in *Ladakhipollenites* as it cannot be satisfactorily placed in any other genus. The original description says this fossil type is psilate-microreticulate. The specimen seen here is more microreticulate than psilate although otherwise the overall characteristics are similar.

*Ladakhipollenites? nanus* sp. nov.

Plate 14, figures 21

**Holotype.** Plate 14, figures 21, sample 22320, EF D-48

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subprolate to prolate; tricolporate, ecto and endocolpi coinciding, 8  $\mu\text{m}$  long, CPi 0.61, borders straight, ends pointed, slightly costate, costae 0.5  $\mu\text{m}$  wide, polar area small, 6  $\mu\text{m}$  wide, endopores circular, simple, rather large in relation to total size of the grain, 2-1 x 2-1  $\mu\text{m}$  wide; walls structure not visible, probably atectate, exine 0.7  $\mu\text{m}$  thick; psilate.

**Dimensions.** Polar diameter 12-(12.5)-13  $\mu\text{m}$ , equatorial diameter 9-(9.5)-10  $\mu\text{m}$ , polar/equatorial 1.31; nm=2, no=19.

**Remarks.** *Psilatricolporites vanus* Dueñas 1983 is bigger (19-29  $\mu\text{m}$ ) and has much smaller pores in relation to the grain size.

**Derivation of name.** After its diminute size.

*Ladakhipollenites? obesus* Hoorn 1993 nov. comb.

**Basionym.** *Psilatricolporites obesus* Hoorn 1993, page 304, plate 2, fig. 20.

Plate 14, figures 22-23

**Holotype.** Plate 14, figures 22-23, sample 22140, EF V-22-2

**Description.** Monad, radial, isopolar, prolate spheroidal; tricolporate, ecto and endocolpi coinciding, short, 8  $\mu\text{m}$  long, CPi 0.47, very thin and almost not visible, borders straight, ends

pointed, costate, costae 1  $\mu\text{m}$  wide, 1  $\mu\text{m}$  thick, restricted to the area on top and bottom of the pores, polar area large, 9  $\mu\text{m}$ , pores quite lalongate, simple, 6 x 1  $\mu\text{m}$  wide; tectate, exine 1  $\mu\text{m}$  thick, nexine 0.3  $\mu\text{m}$  thick, columellae indistinct, 0.3  $\mu\text{m}$  thick, tectum 0.3  $\mu\text{m}$  thick; psilate.

**Dimensions.** Polar diameter 17 $\mu\text{m}$ , equatorial diameter 16  $\mu\text{m}$ , polar/equatorial 1.06; nm=2, no=3.

**Remarks.** *Psilatricolporites* van der Hammen 1956b ex Pierce 1961 is an obligate later synonym of *Tricolporites* van der Hammen 1954 (non Erdtman 1949) because they have the same type species. However, *Tricolpites* is not validly published and a later synonym of *Clethra* as is *Psilatricolporites* (Jansonius and Hills 1976, card 2234). *Ladakhipollenites* Mathur and Jain 1980 accommodates tricolpate psilate pollen grains. This pollen grain is placed provisionally in *Ladakhipollenites* as it cannot be satisfactorily placed in any other genus.

*Ladakhipollenites? pseudonanus* sp. nov.

Plate 14, figures 24

**Holotype.** Plate 14, figures 24, sample 22412, EF D-8-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate to perprolate; tricolporate, colpi long, 14  $\mu\text{m}$  long, CPi 0.77, costate, costae 1  $\mu\text{m}$  wide, 1  $\mu\text{m}$  thick, polar area small, 6  $\mu\text{m}$  wide, endopores lalongate, simple, fairly small in relation to total size of the grain, 1 x 0.5  $\mu\text{m}$  wide; tectate, exine 1.5  $\mu\text{m}$ , sexine 0.4  $\mu\text{m}$  thick, columellae 0.4  $\mu\text{m}$  thick, indistinct, tectum 0.7  $\mu\text{m}$  thick; psilate.

**Dimensions. Dimensions.** Polar diameter 18  $\mu\text{m}$ , equatorial diameter 9  $\mu\text{m}$ , polar/equatorial 2; nm=1, no=1.

**Remarks.** *Psilatricolporites nanus* sp. nov. has very thin exine and larger circular pores.

*Psilatricolporites vanus* Dueñas 1983 is more oblate, has very thin exine and smaller pores in relation to grain size.

**Derivation of name.** After resemblance with *Psilatricolporites nanus* sp. nov.

*Ladakhipollenites? pseudosilvaticus* sp. nov.

Plate 14, figures 25-26

**Holotype.** Plate 14, figures 25-26, sample 22320, EF R-13

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate spheroidal; tricolporate, ecto and endocolpi coinciding, hardly seen, mid-sized, 6 µm long, CPi 0.4, costate, costae 1 µm thick and encircling the whole mesocolpium area, tapering polewards, mesocolpium area is darker due to thicker nexine (costa), polar area large, 8 µm, endopores narrow, lalongate, simple, 5 x 1.5 µm wide; tectate, exine 1 µm, sexine 0.3 µm thick, columellae 0.3 µm thick, indistinct, tectum 0.3 µm thick; psilate to micropitted.

**Dimensions.** Polar diameter 15-(16.5)-18 µm, equatorial diameter 14-(15)-16 µm, polar/equatorial 1.1; nm=2, no=4.

**Remarks.** *L.? silvaticus* (Hoorn 1993) nov. comb. has costate endopores with constriction making them salient on cross section, and polar are is much more rounded than *L.? pseudosilvaticus* sp. nov.

**Derivation of name.** After its resemblance with *L.? silvaticus* (Hoorn 1993) nov. comb.

*Ladakhipollenites? silvaticus* Hoorn 1993 nov. comb.

**Basionym.** *Psilatricolporites silvaticus* Hoorn 1993, page 304, plate 2, fig. 21.

Plate 14, figures 27-28

**Specimens.** Plate 14, figures 27-28, sample 22140, EF S-42

**Description.** Monad, radial, isopolar, subprolate; tricolporate, colpi short, 8  $\mu\text{m}$  long, CPi 0.5, costate, costae 1  $\mu\text{m}$  wide and encircling the whole mesocolpium area, tapering polewards, mesocolpium area is darker due to thicker nexine (costa), pores area slightly protruding; polar area broad, 8  $\mu\text{m}$ , endopores lalongate, simple, 5 x 2  $\mu\text{m}$  wide; tectate, exine 1  $\mu\text{m}$  thick, nexine 0.3  $\mu\text{m}$  thick, columellae 0.3  $\mu\text{m}$  thick, tectum 0.3  $\mu\text{m}$  thick; psilate.

**Dimensions.** Polar diameter 16-(19)-22  $\mu\text{m}$ , equatorial diameter 14-(16.5)-19  $\mu\text{m}$ , polar/equatorial 1.15; nm=2, no=19.

**Remarks.** *Psilatricolporites* van der Hammen 1956b ex Pierce 1961 is an obligate later synonym of *Tricolporites* van der Hammen 1954 (non Erdtman 1949) because they have the same type species; as *Tricolpites* is not validly published and a later synonym of *Clethra*, so is *Psilatricolporites* (Jansonius and Hills 1976, card 2234). *Ladakhipollenites* Mathur and Jain 1980 accommodates tricolpate psilate pollen grains. We place this pollen grain provisionally in *Ladakhipollenites* as it cannot be satisfactorily placed in any other genus.

*Ladakhipollenites? sphericus* sp. nov.

Plate 14, figures 29-30

**Holotype.** Plate 14, figures 29-30, sample 22140, EF X-7-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, spheroidal; tricolporate, ectocolpi long, 14  $\mu\text{m}$  long, CPi 0.73, simple, endocolpi slightly costate, costae 0.5  $\mu\text{m}$  wide, 0.5  $\mu\text{m}$  thick, ends pointed, polar area small, 5  $\mu\text{m}$ , rounded, ectopores circular, simple, large in relation to grain's total size, 5 x 5  $\mu\text{m}$  wide; tectate, exine 1  $\mu\text{m}$ , sexine 0.3  $\mu\text{m}$  thick, columellae 0.3  $\mu\text{m}$  thick, barely distinct, tectum 0.3  $\mu\text{m}$  thick; psilate to micropitted.

**Dimensions.** Polar diameter 16-(17.5)-19  $\mu\text{m}$ , equatorial diameter 16-(17.5)-19  $\mu\text{m}$ , polar/equatorial 1; nm=2, no=2.

**Remarks.** *Psilatricolporites vanus* Gonzalez 1967 has mid-sized colpi and small pores. *P. atalayensis* Hoorn 1993 has much thicker costa and lalongate pores. *P. crassoexinatus* Hoorn 1993 has thicker exine and lalongate pores. *P. magniporatus* Hoorn 1993 has much thicker exine and is more prolate.

**Derivation of name.** After circular pores.

*Ladakhipollenites? xatanawensis* sp. nov.

Plate 15, figures 1-3

**Holotype.** Plate 15, figures 1-3, sample 22140, EF W-35-1

**Paratype.** Plate 15, figures 4, sample 22256, EF O-40-3/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate; tricolporate, ecto and endocolpi coinciding, mid-sized, 25 $\mu\text{m}$  long, CPi 0.67, ends rounded, costate, costae 1  $\mu\text{m}$  wide, 1  $\mu\text{m}$  thick, thinning out towards apocolpia, polar area large, 14  $\mu\text{m}$ , rounded, endopores lalongate, oval to lense-shaped, simple, 8-5 x 4-3  $\mu\text{m}$  wide; tectate, exine 1.5  $\mu\text{m}$ , nexine 0.5  $\mu\text{m}$ , columellae 0.5  $\mu\text{m}$ , indistinct, tectum 0.5  $\mu\text{m}$ , stratification not very clear; psilate. Some grains appear to have atectate psilate apocolpia whereas the mesocolpia is slightly micropitted.

**Dimensions.** Polar diameter 36.5-(36.75)-37  $\mu\text{m}$ , equatorial diameter 20-(20.5)-21  $\mu\text{m}$ , polar/equatorial 1.79; nm=2, no=3.

**Remarks.** *Psilatricolporites cyamus* van der Hammen and Wymstra, 1964 is smaller and thicker and has an equatorial constriction. *P. atalayensis* Hoorn 1993 is thicker, apocolium is acute and pores have a different shape. *P. magniporatus* Hoorn 1993 is thicker, has distinct

columellae and larger pore. *Retitricolporites poriconspectus* Hoorn 1993 is micropitted, of different shape, smaller and has circular pores.

**Derivation of name.** After the indigenous tribe Xatanawa of western Amazonia.

**Genus** *Malvacipolloides* Anzótegui & Garalla 1986

**Type species** *Malvacipolloides densiechinata* Anzótegui & Garalla 1986

*Malvacipolloides dubiosus* sp. nov.

Plate 15, figures 9-10

*Malvacipolloides* sp. 1 Silva-Caminha *et al.* 2010

**Holotype.** Plate 15, figures 9-10, sample 22287, EF L-8

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; tricolporate, colpi very short, 6 µm long, CEi 0.16, simple, almost indistinguishable from pores, pores circular 10 µm wide, simple; tectate, exine 1.5-2 µm thick, nexine 0.6 µm thick, columellae 0.3 µm thick, distinct, tectum 0.6 µm thick; sculpture echinate, spines 4-4 µm tall, 3-3 µm wide at base, 4-6 µm apart, solid and strongly conical, of homogeneous size, spines slightly sunken into tectum, interspines surface micropitted, pits small, circular <0.5 µm wide and distributed evenly over surface of the grain.

**Dimensions.** Polar diameter length 37-(38)-39 µm, polar diameter width 36-(37)-38 µm, length/width 1.02; nm=2, no=9.

**Remarks.** This grain is very similar to *Malvacipolloides maristellae* (Muller *et al.* 1987) Silva-Caminha *et al.* 2010 but differs in spine morphology - *M. maristellae* has raised columellae beneath the spines whereas *M. dubiosus* nov. sp. has a constant columellae thickness. In addition *M. maristellae* has longer spines around the apertures and the spines are bottle shaped, with a rounded base.

**Derivation of name.** After its superficial resemblance to *M. maristellae*.

**Genus** *Margocolporites* Ramanajuan 1966

**Type species** *Margocolporites tsukadai* Ramanajuan 1966

*Margocolporites bilinearis* sp. nov.

Plate 15, figures 13-15

**Holotype.** Plate 15, figures 13-15, sample 22290, EF L-45-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subprolate to prolate; tricolporate, ectocolpi long, 18  $\mu\text{m}$  long, CPi 0.75, ends pointed, marginate, margo produce by fading of the sexine along colpi, margo 2  $\mu\text{m}$  wide, endocolpi costate, costa 1.5-1  $\mu\text{m}$  wide and 1  $\mu\text{m}$  thick, thinning out towards apocolpia; endopores circular 3 x 3  $\mu\text{m}$ , simple; tectate, exine 2  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, columellae 0.5  $\mu\text{m}$  thick, distinct, tectum 0.5  $\mu\text{m}$  thick; sculpture reticulate, lumina 0.5-1.5  $\mu\text{m}$  wide, circular, homobrochate, muri 0.5  $\mu\text{m}$  wide.

**Dimensions.** Polar diameter 24-(25)-26  $\mu\text{m}$ , equatorial diameter 16-(19)-22  $\mu\text{m}$ , polar/equatorial 1.31; nm=2, no=5.

**Remarks.** *Margocolporites vanwijhei* Germeraad *et al.* 1968 has much wider margo and is baculate near colpi. *Siltaria hammenii* Silva-Caminha *et al.* 2010 has indistinct columellae and is micropitted.

**Derivation of name.** After margo running along colpi, resembling two lines.

*Margocolporites carinae* sp. nov.

Plate 15, figures 16-17

**Holotype.** Plate 15, figures 16-17, sample 22140, EF Q-20-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, triangular-obtuse-straight to slightly convex; tricolporate, colpi short, 12  $\mu\text{m}$  long, CEi 0.34, ends pointed, ectocolpi simple, endocolpi costate, with complex costa: part produced by an outward thickening of nexine around colpi (4  $\mu\text{m}$  wide and 3  $\mu\text{m}$  thick), part produced by absence of the nexine around colpi (3  $\mu\text{m}$  wide), and part immediately along colpi by nexine thickening (3  $\mu\text{m}$  wide). Pores circular 4  $\mu\text{m}$  wide, pore characteristics not clear; tectate, exine 1-1.5  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, columellae 0.5  $\mu\text{m}$  thick, distinct, tectum 0.5  $\mu\text{m}$  thick; psilate to finely and irregularly pitted. Mid part of the mesocolpia has a slight depression of the exine. Rare tetracolporate forms have been seen.

**Dimensions.** Polar diameter length 29-(32)-35  $\mu\text{m}$ , polar diameter width 27-(30)-33  $\mu\text{m}$ , length/width 1.06; nm=2, no=4.

**Remarks.** *Margocolporites* sp. 1 Jaramillo and Dilcher 2001 has dense columellae easily seen through tectum. *M. fastigiatus* Silva-Caminha *et al.* 2010 has margo produced by absence of sexine, not nexine and is fastigiate.

**Derivation of name.** After palynologist Carina Hoorn.

**Botanical affinity.** Aspidosperma (Apocynaceae).

*Margocolporites* “*incertus*”

Plate 15, figures 18-19

**Holotype.** Plate 15, figures 18-19, sample 22434, EF N-53-3/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; tricolporate, ectocolpi long, 20  $\mu\text{m}$  long, CEi 0.83, ends rounded, marginate, margo produced by absence of the sexine around colpi, 2  $\mu\text{m}$  wide, endocolpi not very clear, costate, costa 1  $\mu\text{m}$  wide. Pores circular 2 x 2  $\mu\text{m}$  wide,



simple; tectate, exine 1.5  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, columellae 0.5  $\mu\text{m}$  thick, barely distinct, very thin, regularly distributed, tectum 0.5  $\mu\text{m}$  thick; psilate.

**Dimensions.** Polar diameter length 24  $\mu\text{m}$ , polar diameter width 23  $\mu\text{m}$ , length/width 1; nm=1, no=3.

**Remarks.** Left under open nomenclature until more specimens are found to elucidate its morphology.

**Genus** *Paleosantalaceaepites* Biswas 1962 ex Dutta & Sah 1970

**Type species** *Paleosantalaceaepites dinoflagellatus* Biswas 1962 ex Dutta & Sah 1970

*Paleosantalaceaepites invaginatus* sp. nov.

Plate 16, figures 5-6

*Paleosantalaceaepites* sp. 1 Silva-Caminha *et al.* 2010

**Holotype.** Plate 16, figures 5-6, sample 22278, EF S-20

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate; tricolporate, ecto and endocolpi coinciding, long and very thin, 21  $\mu\text{m}$  long, CPi 0.84, costate, costae 1  $\mu\text{m}$  wide, 1  $\mu\text{m}$  thick, borders highly ingavinated, ends pointed, polar area small, 4  $\mu\text{m}$  wide, endocingulate, endocingulum simple, 2.5  $\mu\text{m}$  wide, formed by endopores connecting to each other; tectate, exine 2  $\mu\text{m}$  thick, nexine 0.7  $\mu\text{m}$  thick, columellae 0.7  $\mu\text{m}$  long, distinct, < 0.5  $\mu\text{m}$  apart, tectum 0.7  $\mu\text{m}$  thick; sculpture foveolate, lumina 0.5  $\mu\text{m}$  wide, circular, distributed over the entire surface of the grain, muri 1  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Polar diameter 25-(27)-30  $\mu\text{m}$ , equatorial diameter 17-(17.6)-18  $\mu\text{m}$ , polar/equatorial 1.53; nm=3, no=10.

**Remarks.** *Paleosantalaceaepites distinctus* Jaramillo & Dilcher 2001 has shortcolpi and costate endocingulum. *P. cingulatus* Jaramillo *et al.* 2010 is larger and has a much wider operculate ectocolpi and costate endocingulum.

**Derivation of name.** After invaginating colpi.

*Paleosantalaceaepites kaarsii* Hoorn 1993 nov. comb.

**Basionym.** *Retitricolporites kaarsii* Hoorn 1993, page 305, plate 1, fig. 11-12.

Plate 16, figures 7-8

**Specimens.** Plate 16, figures 7-8, sample 22434, EF E-40

**Description.** Monad, radial, isopolar, spheroidal; tricolporate, ectocolpi and endocolpi coinciding, very thin, almost imperceptible, and short, 12µm long, CPi 0.27, colpi ends pointed, polar area rounded and quite broad, 38 µm wide, marginate, margo produced by a decrease in lumina size around colpi; pores anastomose and form an endocingulum, 2.5 µm wide, costate, costa 5 µm thick, thinning out towards apocolpia; semitectate, exine 3.5 µm thick, nexine 1.5 µm thick, columellae 1.5 µm thick, distinct, 1 µm wide, 1 µm apart, tectum 0.5 µm thick. Reticulate, lumina circular to curvy, 1-5 µm wide, muri 1-1.5 µm wide, simplicolumellate, often smaller lumina ca. 1 µm wide are present on the corners of larger ones.

**Dimensions.** Polar diameter 30-(36.5)-43 µm, equatorial diameter 30-(36)-42 µm, polar/equatorial 1.01; nm=2, no=11.

**Remarks.** *Retitricolporites* (Van der Hammen 1956) Van der Hammen and Wymstra 1964 is invalid and a later synonym of *Viburnum* (Jansonius and Hills 1976, card 2402).

*Paleosantalaceaepites* Biswas 1962 ex Dutta and Sah 1970 accommodates tricolporate pollen grains with long or short colpi and endocingulum. The original description of the holotype

shows a lumina variation from micro (0.5  $\mu\text{m}$ ) to mesoreticulate (2.5  $\mu\text{m}$ ), we have observed more often larger lumina individuals but microreticulation has also been seen.

**Genus** *Ranunculacidites* Sah 1967

**Type species** *Ranunculacidites communis* Sah 1967

*Ranunculacidites reticulatus* sp. nov.

Plate 16, figures 15-17

**Holotype.** Plate 16, figures 15-16, sample 22518, EF L-16-1

**Paratype.** Plate 16, figures 17, sample 22518, EF L-9-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subprolate to prolate spheroidal; tricolporate, ecto and endocolpi coinciding, long and wide, 6-7  $\mu\text{m}$  wide, 17  $\mu\text{m}$  long, CPi 0.56, simple, polar area 7  $\mu\text{m}$ , operculate, operculum as long as colpi, 4  $\mu\text{m}$  wide; pores indistinct; semitectate, exine 2  $\mu\text{m}$ , nexine 1  $\mu\text{m}$ , notably thicker than sexine, columellae 0.5  $\mu\text{m}$ , distinct, 0.5  $\mu\text{m}$  wide, 0.5  $\mu\text{m}$  apart, tectum 0.5  $\mu\text{m}$ ; reticulate, lumina circular, elongate to slightly polygonal, 1  $\mu\text{m}$  wide, muri 0.5  $\mu\text{m}$  thick, homobrochate. Operculum coalesces with grain at colpi extremities in such a way that reticulum of colpi and grain is continuous and has no differentiation of lumina size or shape. Operculum often remains well preserved.

**Dimensions.** Polar diameter 29-(29.5)-30  $\mu\text{m}$ , equatorial diameter 26-(27)-28  $\mu\text{m}$ , polar/equatorial 1.09; nm=2, no=18.

**Remarks.** *Ranunculacidites* Sah 1967 accommodates small, tricolp(or)ate, with variable exine ornamentation and operculum covering colpi entirely or partially. *Ranunculacidites operculatus* (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher 2001 is psilate-micropitted. *Retitricolpites operculatus* Herngreen 1973 is smaller, has larger lumina in comparison to grain size and operculum is psilate.

**Derivation of name.** After reticulate ornamentation.

**Genus** *Retibrevitricolporites* Legoux 1978

**Type species.** *Retibrevitricolporites obodoensis* Legoux 1978 (?)

*Retibrevitricolporites solimoensis* Hoorn 1993 nov. comb.

**Basionym.** *Retitricolporites solimoensis* Hoorn 1993, page 305, plate 2, fig. 12.

Plate 16, figures 20-23

**Specimens.** Plate 16, figures 20-21, sample 22140, EF H-25

**Specimens.** Plate 16, figures 22-23, sample 22140, EF D-10-1/3

**Description.** Monad, radial, isopolar, spheroidal, amb circular; tricolporate, endo and ectocolpi coinciding, very short, 4  $\mu\text{m}$  long, CEi 0.28, simple, borders straight, colpi ends rounded, polar area broad, 11  $\mu\text{m}$  wide; endopores lalongate, 3 x 1.5  $\mu\text{m}$  wide, costate, costa 1  $\mu\text{m}$  wide, restricted to the bottom and top; tectate, exine 1  $\mu\text{m}$  thick, nexine 0.3  $\mu\text{m}$  thick, columellae 0.3  $\mu\text{m}$  thick, distinct, tectum 0.3  $\mu\text{m}$  thick. Microreticulate, lumina circular, < 0.5  $\mu\text{m}$  wide, muri < 0.5  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Equatorial diameter length 14-(14.6)-15  $\mu\text{m}$ , equatorial diameter width 14-(14.6)-15  $\mu\text{m}$ ; length/width 1; nm=3, no=5.

**Remarks.** *Retitricolporites* (Van der Hammen 1956) Van der Hammen and Wymstra 1964 is invalid and a later synonym of *Viburnum* (Jansonius and Hills 1976, card 2402).

*Retibrevitricolporites* Legoux 1978 accommodates retibrevitricolporate pollen grains.

**Genus** *Retitrescolpites* Sah 1967

**Type species** *Retitrescolpites typicus* Sah 1967

*Retitrescolpites benjaminense* sp. nov.

Plate 17, figures 1-4

**Holotype.** Plate 17, figures 1-2, sample 22506, EF H-14

**Holotype.** Plate 17, figures 3-4, sample 22522, EF G-12-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, oblate-spheroidal; tricolporate, ectocolpi simple, 16  $\mu\text{m}$  long, CPi 0.55, CEi 0.87, borders straight, ends rounded, endocolpi costate, costa 2  $\mu\text{m}$  wide and 2  $\mu\text{m}$  thick, polar area 8  $\mu\text{m}$  wide; endopores simple, slightly lologate, 2 x 3  $\mu\text{m}$  wide; semitectate, exine 3  $\mu\text{m}$  thick, nexine < 1  $\mu\text{m}$  thick, columellae 2  $\mu\text{m}$  thick, distinct, 0.5  $\mu\text{m}$  wide, 0.5  $\mu\text{m}$  apart, and double the normal size at the poles, 4  $\mu\text{m}$  thick, tectum very thin, ca. 0.5  $\mu\text{m}$  thick, almost not visible, giving the wall a retipilate appearance on cross section.

Microreticulate, lumina 0.5  $\mu\text{m}$ , elongate to curvimurate, muri 0.5  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Equatorial view: Polar diameter 29  $\mu\text{m}$ , equatorial diameter 29  $\mu\text{m}$ ,

Polar/equatorial 1.

Polar view: Polar diameter length 32  $\mu\text{m}$ , polar diameter width 32  $\mu\text{m}$ , length/width 1; nm=2, no=44.

**Remarks.** *Retitrescolpites* Sah 1967 accommodates retitricolp(or)ate with coarse retipilate or reticulate exine. Its type species, *R. typicus* Sah 1967 is described as having “muri usually sinuous”, in other words curvimurate. *R. baculatus* Jaramillo and Dilcher 2001 is much larger and thicker and tricolpate. *R.? irregularis* (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001, *R. magnus* (Gonzalez, 1967) Jaramillo and Dilcher, 2001, *R. peculiaris* and *R. saturum* Jaramillo and Dilcher 2001 have much coarser reticulum. *R. definidus* Jaramillo *et al.* 2007 has a well-defined costa around colpi.

**Derivation of name.** After the town Benjamin Constant in Amazonas state, Brazil.

*Retitrescolpites grossus* sp. nov.

Plate 17, figures 5-6

**Holotype.** Plate 17, figures 5-6, sample 22503, EF U-8-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subspheroidal, circular amb; tricolporate, ecto and endocolpi coinciding, 30µm long, CPi 0.83, borders invaginated, ends pointed, marginate, margo 2 µm wide, produced by a decrease in columellae thickness and lumina size towards colpi, also costate, costa 2 µm wide and µm thick, thinning out towards apocolpia, polar area small; ecto and endopores coinciding, lolongate, 6 µm x 3 µm wide, costate, costa 1.5 µm wide; semitectate, exine 2.5 µm thick, nexine 1 µm thick, columellae 0.5 µm thick, distinct, 1 µm wide, 1 µm apart, tectum 1 µm thick. Reticulate, lumina 1.5-3 µm, elongate to curvimate, muri 1 µm wide, simplicolumellate, homobrochate.

**Dimensions.** Equatorial view: Polar diameter 36 µm, equatorial diameter 35 µm, Polar/equatorial 1.02. Polar view: Polar diameter length 25-(32)-39 µm, polar diameter width 24-(31)-38 µm length/width 1.03; nm=3, no=32.

**Remarks.** *Retitrescolpites baculatus* Jaramillo and Dilcher 2001 is colpate and larger. *R. ? irregularis* (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001 has wider lumina and costate colpi. *R. magnus* (Gonzalez, 1967) Jaramillo and Dilcher 2001 and *R. saturum* (Gonzalez, 1967) Jaramillo and Dilcher 2001 are colpate.

**Derivation of name.** After its thick wall.

*Retitrescolpites marginatus* sp. nov.

Plate 17, figures 7-9

**Holotype.** Plate 17, figures 7-9, sample 22518, EF N-25-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subprolate; tricolporate, ectocolpi marginate and costate, 22 µm long, CPi 0.70, thin, borders straight, ends rounded, polar area small, 16 µm

wide, margo ca. 2  $\mu\text{m}$  wide, produced by a decrease in lumina size immediately along colpi, costa 2  $\mu\text{m}$  wide, 1  $\mu\text{m}$  thick, interrupted around pores; endopores lalongate, 5  $\mu\text{m}$  x 2  $\mu\text{m}$  wide; tectate, exine 0.5  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$  thick, columellae 0.5  $\mu\text{m}$  thick, distinct, tectum 0.5  $\mu\text{m}$  thick, hardly visible. Suprareticulate, lumina 2-5  $\mu\text{m}$ , highly curvilinear, muri 1  $\mu\text{m}$  wide and 0.5  $\mu\text{m}$  tall, heterobrochate. Reticulum is created by raised muri on top of tectum, meaning muri is not sustained by columellae, but solid.

**Dimensions.** Polar diameter 31  $\mu\text{m}$ , equatorial diameter 27  $\mu\text{m}$ . Polar/equatorial 1.14; nm=1, no=5.

**Remarks.** The combination of suprareticulum with curvimuri has not been described. *R. marginatus* sp. nov. bears some resemblance with *Rhipites guianensis* (Van der Hammen and Wymstra, 1964) Jaramillo and Dilcher, 2001 but the latter has lalongate indistinct pores and wall and reticulate structure are also different (elongated).

**Derivation of name.** After margin of the colpi.

### **Genus** *Rhipites* Wodehouse 1933

**Type species** *Rhipites bradleyi* Wodehouse 1933

*Rhipites caputoi* Hoorn 1993 nov. comb.

**Basionym.** *Retitricolporites caputoi* Hoorn 1993, page 305, plate 3, fig. 1-2.

Plate 17, figures 18-19

**Specimens.** Plate 17, figures 18-19, sample 22412, EF P-12-4

**Description.** Monad, radial, isopolar, prolate; tricolporate, ectocolpi coinciding, mid-sized, 21  $\mu\text{m}$ , CPi 0.66, very thin, borders slightly straight, colpi ends rounded, polar area medium, 13  $\mu\text{m}$  wide, endocolpi costate, costa 1  $\mu\text{m}$  thick and 2  $\mu\text{m}$  wide; pores slightly lalongate, 5  $\mu\text{m}$  x 4  $\mu\text{m}$  wide, simple; tectate, exine 2  $\mu\text{m}$  thick, nexine 0.6  $\mu\text{m}$  thick, columellae 0.8  $\mu\text{m}$  thick, distinct and packed, tectum 0.6  $\mu\text{m}$  thick. Reticulate, lumina circular to slightly

elongate, 1  $\mu\text{m}$  wide, muri 1  $\mu\text{m}$  wide, heterobrochate, lumina decreases slightly towards mesocolpium.

**Dimensions.** Polar diameter 29-(30.8)-32  $\mu\text{m}$ , equatorial diameter 18-(20.3)-22  $\mu\text{m}$ , polar/equatorial 1.51; nm=3, no=44.

**Remarks.** *Retitricolporites* (Van der Hammen 1956) Van der Hammen and Wymstra 1964 is invalid and a later synonym of *Viburnum* (Jansonius and Hills 1976, card 2402). *Rhoipites* Wodehouse 1933 accommodates tricolporate pollen grains that are reticulate-pitted, prolate, with marginate/costate colpi (Jansonius and Hills 1976, card 2421, Pocknall & Crosbie 1982, Frederiksen 1983).

*Rhoipites caricatus* sp. nov.

Plate 17, figures 20-23

**Holotype.** Plate 17, figures 20-21, sample 22164, EF P-7

**Paratype.** Plate 17, figures 22-23, sample 22272, EF S-39

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate spheroidal, amb circular; tricolporate, ectocolpi long, 14  $\mu\text{m}$  long, CEi 0.77, CPi 0.68, marginate, margo produced by thinning of columellae thickness towards colpi, margo 2  $\mu\text{m}$  wide and 1  $\mu\text{m}$  thick, borders slightly invaginated, colpi ends rounded, polar area small, 3  $\mu\text{m}$  wide, endocolpi costate, costa 1  $\mu\text{m}$  thick and 1  $\mu\text{m}$  wide, all along colpi; pores circular to slightly lalongate, 2.5  $\mu\text{m}$  x 2  $\mu\text{m}$  wide, slightly costate, costa 0.5  $\mu\text{m}$  thick; tectate, exine 2  $\mu\text{m}$  thick nexine 0.7  $\mu\text{m}$  thick, columellae 0.7  $\mu\text{m}$  thick, distinct, tectum 0.7  $\mu\text{m}$  thick. Microreticulate, lumina circular to elongate, 0.5-1  $\mu\text{m}$  wide, muri 0.5-1  $\mu\text{m}$  wide, homobrochate.



**Dimensions.** Equatorial view: Polar diameter 16-(17.5)-19  $\mu\text{m}$ , equatorial diameter 15-(15.5)-16  $\mu\text{m}$ . Polar/equatorial 1.12. Polar view: Equatorial diameter length 18  $\mu\text{m}$ , equatorial diameter width 16  $\mu\text{m}$ , length/width 1.12; nm=3, no=9.

**Remarks.** *Retitricolporites milnei* Hoorn 1993 has short colpi, flat, lalongate pores and smaller reticulum. *Siltaria dilcheri* Silva-Caminha *et al.* 2010 is micropitted, has pores with well developed costa and slightly protruding. *Rhoipites crassicosatus* Van der Hammen and Wymstra 1964 nov. comb. Differs in being heterobrochate, foveolate in mesocolpia and in having a much thicker costa endocolpi and simple pores

**Derivation of name.** After ‘caricature’, a drawing which has simplified aspects of an object, in reference to the fact that *R. caricatus* sp. nov. has a very common tricolporate morphology.

*Rhoipites crassicosatus* Van der Hammen and Wymstra 1964 nov. comb.

**Basionym.** *Retitricolporites crassicosatus* Van der Hammen and Wymstra 1964, page 236, plate 1, fig. 7-8.

Plate 17, figures 24-25

**Specimens.** Plate 17, figures 24-25, sample 22140, EF T-17-3

**Description.** Monad, radial, isopolar, prolate spheroidal; tricolporate, ectocolpi mid-sized, 11  $\mu\text{m}$ , CPi 0.68, simple, borders straight, colpi ends pointed, polar area 7  $\mu\text{m}$  wide, endocolpi costate, costa 2  $\mu\text{m}$  wide and 1  $\mu\text{m}$  thick, nexine around costa is decreased in thickness creating a clear contour; pores lalongate, 3  $\mu\text{m}$  x 1.5  $\mu\text{m}$  wide, simple; tectate, exine 1.5  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, columellae 0.5  $\mu\text{m}$  thick, distinct, tectum 0.5  $\mu\text{m}$  thick. Foveo-reticulate, lumina circular, < 0.5-0.5  $\mu\text{m}$  wide, muri 1-1.5  $\mu\text{m}$  wide, being denser in the apocolpia where it is microreticulate, and less dense in the mesocolpium where it is foveolate, heterobrochate.

**Dimensions.** Polar diameter 16  $\mu\text{m}$ , equatorial diameter 14  $\mu\text{m}$ , polar/equatorial 1.14; nm=1, no=2.

**Remarks.** *Retitricolporites* (Van der Hammen 1956) Van der Hammen and Wymstra 1964 is invalid and a later synonym of *Viburnum* (Jansonius and Hills 1976, card 2402). *Rhoipites* Wodehouse 1933 accommodates tricolporate pollen grains that are reticulate-pitted, prolate, with marginate/costate colpi (Jansonius and Hills 1976, card 2421, Pocknall & Crosbie 1982, Frederiksen 1983).

*Rhoipites crassitectatus* sp. nov.

Plate 17, figures 26-27

**Holotype.** Plate 17, figures 26-27, sample 22290, EF M-17

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subprolate; tricolporate, endo and ectocolpi coinciding, 25  $\mu\text{m}$  long, CPi 0.86, borders straight, colpi ends rounded, polar area small, 4  $\mu\text{m}$  wide, costate, costa 2  $\mu\text{m}$  wide and 1.5  $\mu\text{m}$  thick, along entire colpi; ectoapores circular, 4 x 4  $\mu\text{m}$  wide, simple; tectate, exine 3  $\mu\text{m}$  thick, nexine 0.7  $\mu\text{m}$  thick, columellae 0.7  $\mu\text{m}$  thick, distinct, well spaced, tectum 1.5  $\mu\text{m}$  thick. Micropitted, pits circular, <0.5  $\mu\text{m}$  wide, muri ca. 0.5  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Polar diameter 29  $\mu\text{m}$ , equatorial diameter 24  $\mu\text{m}$ , polar/equatorial 1.2; nm=1, no=1.

**Remarks.** *Retitricolporites crassopolaris* Hoorn 1994 has thicker exine in polare areas and is thinner. *R. poriconspectus* Hoorn 1994 has indistinct columellae and broader apocolpium. *Foveotricolporites crassiexinus* van Hoeken-Klinkenberg 1966 is foveolate, has much wider lumina.

**Derivation of name.** After its thick tectum.

*Rhoipites crassnexinicus* sp. nov.

Plate 18, figures 1-4

**Holotype.** Plate 18, figures 1-3, sample 22158, EF P-46-4

**Paratype.** Plate 18, figures 4, sample 22158, EF N-38-3/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate spheroidal; tricolporate, endo and ectocolpi coinciding, 18 µm long, CPi 0.81, ectocolpi simple, borders straight, colpi ends rounded, polar area small, 8 µm wide, endocolpi costate, costa 2 µm wide and 1.5 µm thick, along entire colpi and very gently thinning out towards apocolpia; ectocolpi has a slight constriction at the equator that is mirrored by the costa endocolpi shape that is absent in the pores area; endopores lalongate, simple, 4 µm x 1.5 µm wide; tectate, exine 1.5 µm thick at apocolpia and 3 µm thick at mesocolpia, nexine 1 µm thick at apocolpia and 2 µm thick at mesocolpia, columellae 0.5-0.3 µm thick, distinct, tectum 0.5-0.3 µm thick. Microreticulate, lumina circular to elongate, 0.5 µm wide, muri 0.5 µm wide, homobrochate.

**Dimensions.** Polar diameter 22-(23)-24 µm, equatorial diameter 20 µm. Polar/equatorial 1.15; nm=2, no=2.

**Remarks.** *Retitricolpites colpiconstrictus* Hoorn 1994 is tricolpate and has different exine.

**Derivation of name.** After thick nexine.

*Rhoipites guttus* sp. nov.

Plate 18, figures 7-8

**Holotype.** Plate 18, figures 7-8, sample 22277, EF H-39-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, spheroidal; tricolporate, ectocolpi medium-sized, 12  $\mu\text{m}$ , CPi 0.54, simple, borders straight, colpi ends rounded, very thin, polar area broad, 10  $\mu\text{m}$  wide, endocolpi costate, costa 1.5  $\mu\text{m}$  wide and 2.5  $\mu\text{m}$  thick, turned inwards, restricted to the bottom and top side of pore, endopores large, lalongate, 6 x 3.5  $\mu\text{m}$  wide, simple; tectate, exine 1.6  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$ , columellae 0.3  $\mu\text{m}$  thick, distinct, well spaced, tectum 0.3  $\mu\text{m}$  thick. Reticulate, lumina circular to elongate, 1-2  $\mu\text{m}$  wide, muri < 1  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Polar diameter 22-(24)-26  $\mu\text{m}$ , equatorial diameter 22-(24)-26  $\mu\text{m}$ , polar/equatorial 1; nm=2, no=2.

**Remarks.** *Retitricolporites oblatius* Hoorn 1994 is micropitted and has narrow pores.

*Retibrevitricolporites solimoensis* Hoorn 1993 nov. comb. Is much smaller.

**Derivation of name.** From the Latin ‘gutta’ meaning drop, after the costa shape in lateral view.

*Retitricolporites nanus* sp. nov.

Plate 18, figures 9-10

**Holotype.** Plate 18, figures 9-10, sample 22287, EF T-17-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate, very small; tricolporate, endo and ectocolpi coinciding, long, 12  $\mu\text{m}$  long, CPi 0.75, ectocolpi simple, borders straight, colpi ends pointed, polar area small, 2  $\mu\text{m}$  wide, endocolpi costate, costa 0.5-1  $\mu\text{m}$  wide and 0.5-1  $\mu\text{m}$  thick; pores very large in relation to grain size, slightly lalongate, simple, 3  $\mu\text{m}$  x 2.5  $\mu\text{m}$  wide; tectate, exine 1  $\mu\text{m}$  thick, nexine 0.4  $\mu\text{m}$ , columellae 0.2  $\mu\text{m}$  thick, indistinct, tectum 0.4  $\mu\text{m}$  thick. Reticulate, lumina circular to elongate, 1  $\mu\text{m}$  wide, muri 1  $\mu\text{m}$  wide, homobrochate. Often, but not always, seen in clumps.

**Dimensions.** Polar diameter 16-(17)-18  $\mu\text{m}$ , equatorial diameter 10-(11)-12  $\mu\text{m}$ , polar/equatorial 1.54; nm=2, no=4.

**Derivation of name.** After its very small size.

*Rhoipites oblatas* Hoorn 1994 nov. comb.

Plate 18, figures 11-12

**Basionym.** *Retitricolporites oblatas* Hoorn 1994, page 39, plate 3, fig. 11-12.

**Specimens.** Plate 18, figures 11-12, sample 22290, EF S-45

**Description.** Monad, radial, isopolar, oblate to oblate spheroidal; tricolporate, endo and ectocolpi coinciding, mid-sized, 12  $\mu\text{m}$  long, CPi 0.63, ectocolpi simple, borders slightly invaginated, colpi ends pointed, polar area broad, 6  $\mu\text{m}$  wide, endocolpi costate, costa 2-0.5  $\mu\text{m}$  wide and 2.5-1  $\mu\text{m}$  thick, much thicker around equator, turned inwards and gradually thinning out towards apocolpia, almost conical shaped and partially extending around pores; endopores lalongate, 4.5  $\mu\text{m}$  x 2  $\mu\text{m}$  wide, simple; tectate, exine 1.5  $\mu\text{m}$  thick, nexine 0.6  $\mu\text{m}$  thick, columellae 0.3  $\mu\text{m}$  thick, distinct, tectum 0.6  $\mu\text{m}$  thick. Microreticulate, lumina circular, 0.5  $\mu\text{m}$  wide, muri 0.5  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Polar diameter 18-(19.5)-21.5  $\mu\text{m}$ , equatorial diameter 16-(17.5)-18.5  $\mu\text{m}$ , polar/equatorial 1.11; nm=3, no=17.

**Remarks.** *Retitricolporites* (Van der Hammen 1956) Van der Hammen and Wymstra 1964 is invalid and a later synonym of *Viburnum* (Jansonius and Hills 1976, card 2402). *Rhoipites* Wodehouse 1933 accommodates tricolporate pollen grains that are reticulate-pitted, prolate, with marginate/costate colpi (Jansonius and Hills 1976, card 2421, Pocknall & Crosbie 1982, Frederiksen 1983).

*Rhoipites poropartitus* sp. nov.

Plate 18, figures 13-14

**Holotype.** Plate 18, figures 13-14, sample 22386, EF T-10-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate; tricolporate, ecto and endocolpi coinciding, long, 32  $\mu\text{m}$ , CPi 0.76, ectocolpi simple, borders straight, colpi ends rounded, polar area small, 4  $\mu\text{m}$  wide, endocolpi costate, costa 1  $\mu\text{m}$  wide and 1  $\mu\text{m}$  thick; endopores discrete, circular, simple, 4  $\mu\text{m}$  x 3 wide, part of the costa endocolpi runs through pores giving the impression that pores are split in two; semitectate, exine 2  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$ , columellae 0.7  $\mu\text{m}$  thick, distinct, tectum 0.3  $\mu\text{m}$  thick, not very clear. Reticulate, lumina circular to polygonal, 1  $\mu\text{m}$  wide, muri 1  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Polar diameter 42  $\mu\text{m}$ , equatorial diameter 30  $\mu\text{m}$ , polar/equatorial 1.4; nm=1, no=1.

**Remarks.** *Retitricolporites wijmstrae* Hoorn, 1994 has large, lalongate pores and is thicker.

**Derivation of name.** After pores appearing split.

*Rhoipites protoguttus* sp. nov.

Plate 18, figures 15-17

**Holotype.** Plate 18, figures 15, sample 22518, EF M-17-3

**Paratype.** Plate 18, figures 16-17, sample 22522, EF O-13-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, oblate spheroidal to prolate spheroidal, amb circular; tricolporate, endo and ectocolpi coinciding, mid-sized, 20  $\mu\text{m}$  long, CPi 0.64, CEi 0.66, very thin, ectocolpi marginate, margo discrete, only seen in polar view, created by a thickening of columellae around colpi, from 0.3 to 0.5  $\mu\text{m}$  thick, borders very slightly invaginating, ends rounded, polar area broad, 15-13  $\mu\text{m}$  wide, endocolpi simple; endopores very large, lalongate,

lense shapes with beak-like extremities, 10  $\mu\text{m}$  x 6  $\mu\text{m}$  wide, costate, costa restricted to bottom and top of pores, 1  $\mu\text{m}$  wide and 2  $\mu\text{m}$  thick, turned inwards; tectate, exine 2  $\mu\text{m}$  thick, nexine 0.3  $\mu\text{m}$ , columellae 0.3  $\mu\text{m}$  thick, distinct, tectum 0.3  $\mu\text{m}$  thick. Microreticulate to micropitted, lumina circular, 0.5  $\mu\text{m}$  wide, muri 0.5-1  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Equatorial view: polar diameter 31-(33)-35  $\mu\text{m}$ , equatorial diameter 32-(32.5)-33  $\mu\text{m}$ , polar/equatorial 1.01. Polar view: equatorial diameter length 36, equatorial diameter width 36, length/width 1; nm=3, no=6.

**Remarks.** *Retitricolporites wijmstrae* Hoorn 1994 has long costate colpi and wall structure is different. *R. crassopolaris* Hoorn 19994 has thicker wall at apocolpia.

**Derivation of name.** After resemblance to *R. guttus* sp. nov.

*Rhoipites pseudocrassopolaris* sp. nov.

Plate 18, figures 18-19

**Holotype.** Plate 18, figures 18-19, sample 22140, EF W-10-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate; tricolporate, endo and ectocolpi coinciding, long, 17  $\mu\text{m}$ , CPi 0.7, ectocolpi simple, colpi borders straight, ends rounded, polar area small, 3  $\mu\text{m}$  wide, endocolpi costate, costa 1.5  $\mu\text{m}$  wide and 1.5  $\mu\text{m}$  thick, thinning out towards apocolpia; endopores lalongate, 4  $\mu\text{m}$  x 2  $\mu\text{m}$  wide, simple, abruptly protruding; tectate, polar area is thicker due to a gradual thickening of the columellae from mesocolpium to apocolpium, exine 1.5  $\mu\text{m}$  thick at mesocolpia and 2.5  $\mu\text{m}$  thick at apocolpia, nexine 0.5  $\mu\text{m}$ , columellae 0.5  $\mu\text{m}$  thick at mesocolpia and 1.5  $\mu\text{m}$  thick at apocolpia, distinct, very thin, < 0.5  $\mu\text{m}$  wide, tectum 0.5  $\mu\text{m}$  thick. Micropitted, lumina circular, 0.5  $\mu\text{m}$  wide, muri 0.5-1  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Polar diameter 24  $\mu\text{m}$ , equatorial diameter 16  $\mu\text{m}$ . Polar/equatorial 1.5; nm=1, no=1.

**Remarks.** *Retitricolporites crassopolaris* Hoorn 1994 has a different wall structure, lacks protruding pores and nexine rather than columellae is what makes polar areas thicker.

**Derivation of name.** After false resemblance to *Retitricolporites crassopolaris* Hoorn 1994.

*Rhoipites pseudopilatus* sp. nov.

Plate 18, figures 20-21

**Holotype.** Plate 18, figures 20-21, sample 22320, EF L-44-3/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate; tricolporate, ecto and endocolpi coinciding, long, 16  $\mu\text{m}$ , CPi 0.69, ectocolpi simple, colpi borders invaginated, ends rounded, polar area small, 4  $\mu\text{m}$  wide, ectocolpi costate, costa 2  $\mu\text{m}$  wide and 2  $\mu\text{m}$  thick; ecto and endopores coinciding, large, lolongate, 9  $\mu\text{m}$  x 4  $\mu\text{m}$  wide, simple; tectate, exine 1  $\mu\text{m}$  thick, nexine 0.3  $\mu\text{m}$ , columellae 0.4  $\mu\text{m}$  thick, distinct, regularly distributed, 0.3  $\mu\text{m}$  wide, 0.3  $\mu\text{m}$  apart, tectum 0.3  $\mu\text{m}$  thick. In cross section, wall appears to be pilate, but true tectum forms. Microreticulate, lumina circular, 0.5-1  $\mu\text{m}$  wide, muri 0.5-1  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Polar diameter 21-(22)-23  $\mu\text{m}$ , equatorial diameter 16-(17)-18  $\mu\text{m}$ , polar/equatorial 1.43-1.29; nm=2, no=2.

**Remarks.** Very few retitricolporate grains are described as lolongate. *Foveotricolporites lolongatis* sp. nov. is psilate-micropitted with different wall structure.

**Derivation of name.** After false pilate appearance.

*Rhoipites ticunaensis* sp. nov.

Plate 18, figures 22-25



**Holotype.** Plate 18, figures 22-23, sample 22349, EF D-40-2

**Paratype.** Plate 18, figures 24-25, sample 22456, EF Q-7-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, spheroidal, amb triangular-obtuse-straight. Grains are mostly found in oblique view, where shape is somewhat pentagonal; tricolporate, ecto and endocolpi coinciding, colpi mid-sized, 12  $\mu\text{m}$  long, CPi 0.76, CEi 0.57, ectocolpi simple, colpi borders invaginated, ends rounded, polar area 6  $\mu\text{m}$  wide, endocolpi costate, costa 1.5  $\mu\text{m}$  wide and 1.5  $\mu\text{m}$  thick; endopores circular, 3  $\mu\text{m}$  x 3  $\mu\text{m}$  wide, atriate, atrium circular and simple, 6 x 6  $\mu\text{m}$  wide; tectate, exine 2  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$ , columellae 0.5  $\mu\text{m}$  thick, distinct, tectum 0.5  $\mu\text{m}$  thick. Reticulate, lumina circular to polygonal, with two size modes: in the apocolpia there are larger lumina (1-2  $\mu\text{m}$  wide) usually surrounded by smaller lumina (0.5  $\mu\text{m}$  wide) what does not seem to happen in the mesocolpia, homobrochate, muri 0.5-1  $\mu\text{m}$  thick. When seen in equatorial view (rarely), each mesocolpium has a markedly trapezoidal shape.

**Dimensions.** Equatorial view: polar diameter 21  $\mu\text{m}$ , equatorial diameter 21  $\mu\text{m}$ , polar/equatorial 1.

Polar view: equatorial diameter length 20-(20.5)-21  $\mu\text{m}$ , equatorial diameter width 18-(18.5)-19  $\mu\text{m}$ , length/width 1.10; nm=3, no=18.

**Remarks.** Botanical affinity: *Schefflera/Didymopanax* (Araliaceae). *Byttneripollis rudeae* Silva-Camina *et al.* 2010 and *B. rugulata* sp. nov. are also atriate, but are triporate and overall morphology differs significantly.

**Derivation of name.** After the western Amazonia indigenous tribe Ticuna.

*Rhoipites toigoi* sp. nov.

Plate 19, figures 1-4

**Holotype.** Plate 19, figures 1-3, sample 22422, EF Q-21-2

**Paratype.** Plate 19, figures 4, sample 22386, EF L-43-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate spheroidal to spheroidal; tricolporate, ectocolpi med-sized, 15 µm long, CPi 0.5, simple, very thin and sometimes not visible; colpi borders straight, ends rounded, polar area large, 10 µm wide; endopores lalongate, 9 µm x 2 µm wide, costate, costa restricted to bottom and top of pores, 3 µm wide and 2 µm wide thick; tectate, exine 2.5 µm thick, nexine 1 µm, columellae 1 thick, distinct, very thin and regularly distributed, tectum 0.5 µm thick. Suprareticulate, coarse reticulation, lumina large, circular, 2-3 µm wide, muri thick, 1.5 µm wide, homobrochate, smaller lumina (ca. 1 µm wide) appear within the muri, usually at lumina corners. Reticulum short, formed by raised tectum, which has an undulating appearance in cross section, intraluminal surface psilate.

**Dimensions.** Polar diameter 30-(36)-42 µm, equatorial diameter 30-(33.5)-37 µm, polar/equatorial 1-1.07; nm=2, no=5.

**Remarks.** This grain bears resemblance to *R.? pluricolumellatus* sp. nov., but it is tricolporate and has much shorter and less conspicuous colpi. *Retitricolporites wijmstrae* Hoorn 1994 has long costate colpi and wall structure is different.

**Derivation of name.** After Brazilian palynologist Marleni Toigo.

### **Genus** *Striatopollis* Krutzsch 1959

**Type species** *Striatopollis sarstedtensis* Krutzsch 1959

*Striatopollis macrolobium* sp. nov.

Plate 20, figures 3-5

**Holotype.** Plate 20, figures 3-4, sample 22140, EF Q-7-3

**Holotype.** Plate 20, figures 5, sample 22282, EF H-11-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate; tricolporate, ecto and encolpi coinciding, very long and wide, 30µm long, CPI 0.9, simple, colpi borders invaginated, ends open, polar area very small to absent; endopores circular, 3-4 µm x 3-4 µm wide, simple, not easily visible; tectate, exine 2.5 µm thick, nexine 0.3 µm, columellae 0.3 µm thick, distinct, very short in relation to tectum, dense and regularly distributed, tectum 2 µm thick. Striate, striae solid, running parallel to the polar axis, 1.5 µm wide, 0.5 µm apart, interstriae surface psilate. Some striae can be shorter near the colpi, hence not connecting pole to pole as most striae.

**Dimensions.** Polar diameter 29.5-(31.25)-33 µm, equatorial diameter 17-(19)-21 µm, polar/equatorial 1.64; nm=2, no=13.

**Remarks.** Similar to *Striatopollis catatumbus* (Gonzalez, 1967) Takahashi and Jux, 1989 but with distinctive thicker tectum/striae and a clearly different relation of columellae-tectum thicknesses.

**Derivation of name.** After the extant Fabaceae genus *Macrolobium*, to which the fossil type bears resemblance.

### **Genus** *Verrutricolporites* van der Hammen & Wijmstra 1964

**Type species** *Verrutricolporites rotundiporus* van der Hammen & Wijmstra 1964

*Verrutricolporites pequenus* sp. nov.

Plate 20, figures 10-11

**Holotype.** Plate 20, figures 10-11, sample 22140, EF N-37

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subprolate; tricolporate, ectocolpi mid-sized, 10 µm long, CPI 0.64, thin, simple, colpi borders straight, ends pointed, polar area broad and rounded, 4 µm wide; endopores lalongate, relatively large, 4 µm x 2.5 µm wide, simple;

tectate, exine relatively thick, 2.1  $\mu\text{m}$  thick, nexine 1.5  $\mu\text{m}$ , columellae 0.3 thick, barely distinct, tectum 0.3  $\mu\text{m}$  thick. Verrucate, verrucae very short and of irregular shape, ca. 1  $\mu\text{m}$  wide, < 0.5  $\mu\text{m}$  tall, 0.5-1  $\mu\text{m}$  apart. A few larger verrucae are spread over the grain's surface.

**Dimensions.** Polar diameter 15.5-(15.75)-16  $\mu\text{m}$ , equatorial diameter 13-(13.5)-14  $\mu\text{m}$ , polar/equatorial 1.16; nm=2, no=2.

**Remarks.** *Verrutricolporites rotundiporus* Van der Hammen and Wymstrae 1964 has smaller and circular pore, and a smaller ration of verruca and grain sizes.

**Derivation of name.** From the Portuguese word 'pequeno', meaning small.

*Verrutricolporites simplex* sp. nov.

Plate 20, figures 14-17

**Holotype.** Plate 20, figures 14-15, sample 22482, EF F-10

**Paratype.** Plate 20, figures 16-17, sample 22481, EF F-48

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate spheroidal, amb subtriangular; tricolporate, colpi long, 14  $\mu\text{m}$  long, CPi 0.77, colpi borders slightly invaginated, ends rounded, simple; pores lolongate, 4 x 3  $\mu\text{m}$  long, slightly costate, costa ca. 1  $\mu\text{m}$  wide; intectate, exine 2-3  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$ , sexine 2  $\mu\text{m}$  thick. Verrucate, verrucae rounded, 2  $\mu\text{m}$  wide, 2  $\mu\text{m}$  tall, ca. 1  $\mu\text{m}$  apart. Verrucae of constant size and shape.

**Dimensions.** Polar diameter 18  $\mu\text{m}$ , equatorial diameter 17, polar/equatorial 1.05.

Polar diameter length 16  $\mu\text{m}$ , equatorial diameter width 20  $\mu\text{m}$ , length/diameter 0.8; nm= 2, no=3.

**Remarks.** *Verrutricolporites haplites* Gonzalez 1967 is larger has costate colpi and irregular verrucae. *V. rotundiporus* Van der Hammen and Wymstra, 1964 is tectate, with clearly

distinct columellae, has shorter verrucae, indistinct colpi and circular pore. *V. pequenus* sp. nov. is tectate and has larger lalongate pore.

**Derivation of name.** After the rather simple morphology.

### **Triporate**

**Genus** *Byttneripollis* Konzalová 1976

**Type species** *Byttneripollis coronarius* Konzalová 1976

*Byttneripollis rugulata* sp. nov.

Plate 20, figures 22-25

**Holotype.** Plate 20, figures 22-23, sample 22277, EF L-13-3

**Paratype.** Plate 20, figures 24-25, sample 22158, EF G-20-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular amb; triporate, ectopores circular, 4-5 µm wide, aspidate, aspis 2 µm tall, endopores simple; tectate, exine 1.8 µm thick, nexine 0.6 µm thick, columellae 0.6 µm thick, indistinct, tectum 0.6 µm thick, undulating, which creates a fine rugulate ornamentation; micropits also seen with irregular distribution. Rugulae ca. 0.5 µm wide, very short and of irregular length.

**Dimensions.** Polar diameter length 26-(27)-28 µm, polar diameter width 25-(25.5)-26 µm; length/width 1.05; nm=2, no=3.

**Remarks.** *Byttneripollis* Konzalová 1976 accommodates 3-6 porate grains with a fringe-like aspis (thickening around pores). *B. ruadae* Silva-Caminha *et al.* 2010 is triangular-obtuse in shape, reticulate endopores costate and has higher aspis around pores than *B. rugulata* sp. nov.

**Derivation of name.** After rugulate pattern.

**Genus** *Foveotriporites* Gonzales-Guzman 1967

**Type species** *Foveotriporites hammenii* Gonzales-Guzman 1967

*Foveotriporites? nodus* sp. nov.

Plate 21, figures 5-6

**Holotype.** Plate 21, figures 5-6, sample 22253, EF F-38-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, triangular amb, apices are folded forming small nodular structures; triporate, pores indistinct. Tectate, exine 1  $\mu\text{m}$  thick, nexine 0.4  $\mu\text{m}$  thick, columellae 0.2  $\mu\text{m}$  thick, indistinct, tectum 0.4  $\mu\text{m}$  thick, perforated, micropitted; micropits circular, <0.5  $\mu\text{m}$  wide, 0.5  $\mu\text{m}$  apart, homobrochate.

**Dimensions.** Polar diameter length 26  $\mu\text{m}$ , polar diameter width 23  $\mu\text{m}$ , length/width 1.13; nm=1, no=1.

**Remarks.** *Proteacidites triangulatus* Lorente 1986 has large, clear pores and is thicker.

*Byttneripollis* species are atriate.

**Derivation of name.** After node-like, or nodular apertures area.

**Genus** *Proteacidites* Cookson 1950 ex Couper 1953 emend.

**Type species** *Proteacidites adenantoides* Cookson 1950

*Proteacidites poriscabratus* sp. nov.

Plate 21, figures 7-9

**Holotype.** Plate 21, figures 7-8, sample 22330, EF G-41-1

**Paratype.** Plate 21, figures 9, sample 22326, EF C-20-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, triangular amb; triporate, pores distinct, circular, 3  $\mu\text{m}$  wide, annulate, annulus produced by a dense scabrate cover around pores, 2  $\mu\text{m}$  wide, 1  $\mu\text{m}$

thick; intectate, exine 0.8  $\mu\text{m}$  thick, nexine 0.5, scabrate, scabrae circular, 0.3  $\mu\text{m}$  tall, <0.5  $\mu\text{m}$  wide, densely and evenly distributed.

**Dimensions.** Polar diameter length 30-(32.5)-35  $\mu\text{m}$ , polar diameter width 24-(27.5)-31  $\mu\text{m}$ , length/width 1.18; nm=2, no=2.

**Remarks.** *Proteacidites triangulatus* Lorente 1986 has large, clear pores and is thicker. *P. dehaani* Germeraad *et al.* 1968 is reticulate. *P. miniporatus* van Hoeken-Klinkenberg, 1966 has very slight scabration and simple, smaller pores.

**Derivation of name.** After scabrae around apertures.

*Proteacidites pseudodehaani* sp. nov.

Plate 21, figures 10

**Holotype.** Plate 21, figures 10, sample 22412, EF L-9-1/3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, triangular amb; triporate, pores distinct, circular, 7  $\mu\text{m}$  wide, annulate, annulus produced by a thickening of the endexine, 3  $\mu\text{m}$  wide, 1  $\mu\text{m}$  thick, and then by a thinning of the endexine 2  $\mu\text{m}$  wide; tectate, exine 1.5  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$  thick, columellae 0.3  $\mu\text{m}$  thick, barely distinct, tectum 0.3  $\mu\text{m}$  thick; microreticulate, lumina circular, 0.5-1  $\mu\text{m}$  wide, muri 0.5-1  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Polar diameter length 31-(34.5)-38  $\mu\text{m}$ , polar diameter width 28-(31)-34  $\mu\text{m}$ , length/width 1.11; nm=2, no=3.

**Remarks.** *P. dehaani* Germeraad *et al.* 1968 has smaller pores, relative thicker annulus and is heterobrochate. *Proteacidites miniporatus* van Hoeken-Klinkenberg 1966 is scabrate and has smaller pores. *P. triangulatus* Lorente 1986 is thicker and micropitted.

**Derivation of name.** After close similarity to *P. dehaani* Germeraad *et al.* 1968.

**Genus** *Psilatриporites* (van der Hammen) Mathur 1966

**Type species** *Psilatриporites inornatus* (van der Hammen) Mathur 1966

*Psilatриporites minimum* sp. nov.

Plate 21, figures 13-14

**Holotype.** Plate 21, figures 13, sample 22506, EF S-4-3

**Paratype.** Plate 21, figures 14-15, sample 22303, EF U-22-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, spheroidal, circular amb; triporate, pores distinct, circular, 3  $\mu\text{m}$  wide, slightly sunken, slightly costate, costa  $<1 \mu\text{m}$ ; atectate, exine 1  $\mu\text{m}$  thick, psilate.

**Dimensions.** Equatorial view: polar diameter 14  $\mu\text{m}$ , equatorial diameter 13  $\mu\text{m}$ , polar/equatorial 1.07,

Polar view: polar diameter length 19  $\mu\text{m}$ , polar diameter width 15  $\mu\text{m}$ , length/width 1.26; nm=2, no=3.

**Remarks.** *Momipites* spp. and *Triporopollenites* spp. have triangular amb and slightly protruding pores. *Psilatриporites sarmientoi* Hoorn 1993 have much larger pores in relation to the grains size. *P. corstanjei* Hoorn 1993 have larger pores with thick annulus.

**Derivation of name.** After diminute size.

**Botanical affinity.** Moraceae/Urticaceae (?).

*Psilatриporites salafrarius* sp. nov.

Plate 21, figures 16-17

**Holotype.** Plate 21, figures 16-17, sample 22460, EF X-8-3

**Paratype.** Plate 21, figures 18, sample 22460, EF V-7-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.



**Description.** Monad, radial, isopolar, subprolate, triangular amb; triporate, endo and ectopores coinciding, 2.5 x 2.5  $\mu\text{m}$  wide, circular, simple, slightly protruding. In equatorial view, there seems to be colpi as well, with invaginated mesocolpia; tectate, exine 1.5  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, columellae distinct, 0.5  $\mu\text{m}$  thick, tectum 0.5  $\mu\text{m}$  thick, psilate to finely micropitted.

**Dimensions.** Polar diameter 20-(20.5)-21  $\mu\text{m}$ , equatorial diameter 17  $\mu\text{m}$ , polar/equatorial 1.20; nm=2, no=51.

**Remarks.** *Florschuetzia trilobata* Germeraad *et al.* 1968 is strongly lobate, i.e., each mesocolpium is highly invaginated, which does not happen in *P. salafrarius* sp. nov. *P. sarimontoi* and *P. costanjei* Hoorn 1993 are circular. *P. desilvae* Hoorn 1993 has pseudocolpi along with pores.

**Derivation of name.** From the Brazilian word ‘salafrário’ meaning ‘deceiver’, as the grain makes one think it is tricolporate but there are no colpi.

### **Genus** *Retitriporites* Ramanujam 1966

**Type species** *Retitriporites curvimurati* Ramanujam 1966

*Retitriporites discretus* sp. nov.

Plate 21, figures 19-22

**Holotype.** Plate 21, figures 19-20, sample 22518, EF V-17

**Paratype.** Plate 21, figures 21-22, sample 22522, EF S-47-1/2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular to subtriangular amb; triporate, endo and ectopores coinciding, 2  $\mu\text{m}$  wide, circular, slightly protruding, annulate, annulus produced by thickening of the endexine, 3  $\mu\text{m}$  wide, 2  $\mu\text{m}$  tick; tectate, exine 2  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$  thick, columellae distinct, 0.5  $\mu\text{m}$  thick, tectum 0.5  $\mu\text{m}$  thick, fossu-reticulate. Some lumina

are circular, 0.5-1  $\mu\text{m}$  wide, but most form fossulae, variable in size, muri 0.5-1  $\mu\text{m}$  wide.

Homobrochate.

**Dimensions.** Polar diameter length 23.5  $\mu\text{m}$ , equatorial diameter width 18-(19.5)-21  $\mu\text{m}$ , length/width 1.2; nm=2, no=2.

**Remarks.** *Retitriporites dubiosus* Gonzalez 1967, *R. poricostatus* Jaramillo and Dilcher 2001, *R. typicus* Gonzalez 1967 and *R. simplex* van der Kaars 1983 all reticulate and have much larger lumina. *R. acostai* Dueñas 1986 is heterobrochate and has larger pores.

**Derivation of name.** After simple morphology.

*Retitriporites tuberosum* sp. nov.

Plate 22, figures 1-2

**Holotype.** Plate 22, figures 1-2, sample 22290, EF F-42-2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subtriangular amb; triporate, endo and ectopores coinciding, 5-6  $\mu\text{m}$  wide, circular, simple, pore outline irregular, highly protruding almost like tubular appendages. Tectate, exine 1.5  $\mu\text{m}$  thick, nexine 0.6  $\mu\text{m}$  thick, columellae indistinct, 0.3  $\mu\text{m}$  thick, tectum 0.6  $\mu\text{m}$  thick; reticulate, lumina of irregular shape and size, circular to elongate, 1-3  $\mu\text{m}$  wide, muri 1.5  $\mu\text{m}$  wide, smaller and circular lumina at apocolpia and larger, more elongate lumina at mesocolpia, heterobrochate.

**Dimensions.** Polar diameter length 35-(36.5)-38  $\mu\text{m}$ , equatorial diameter width 30-(34)-38  $\mu\text{m}$ , length/width 1.07; nm=2, no=2.

**Remarks.** *Byttneripollis* spp have atrium, different from the simple protusions in *R. tuberosum* sp. nov.

**Derivation of name.** After highly protruding apertures, like tubes.

## **Pantocolpate**

**Genus** *Lymingtonia* Erdtman 1960

**Type species** *Lymingtonia rhetor* Erdtman 1960

*Lymingtonia amazonica* sp nov.

Plate 22, figures 5-6

**Holotype.** Plate 22, figures 5-6, sample 22278, EF O-32

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular to slightly quadrangular; pantocolpate, ecto and endocolpi coinciding, 6-colpate (4 colpi around equator and 1 in each apocolpium), 8 µm long, 2 µm wide, slightly sunken, CEi 0.36, ends rounded, colpi costate, costae thin, 0.5 µm thick, 0.5 µm wide; tectate, exine 2 µm thick, endexine 0.7 µm thick, columellae 0.7 µm thick, very thin and regularly distributed, tectum 0.7 µm thick; sculpture psilate, columellae tips seen through tectum.

**Dimensions.** Equatorial diameter length 22-(23)-24 µm, equatorial diameter width 21-(22)-23 µm, length/width 1.04; nm=2, no=2.

**Remarks.** *Lymingthgonia* Erdtman 1960 accommodates pantocolpate pollen. So far the only pantocolpate form described in northern southamerica is *Lymingtonia*? sp. 1 Jaramillo and Dilcher 2001, it is intectate-echinate.

**Derivation of name.** After Amazonia.

*Lymingtonia splendens* sp nov.

Plate 22, figures 7-8

**Holotype.** Plate 22, figures 7-8, sample 22506, EF O-48-3/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; pantocolpate, ecto and endocolpi coinciding, 16-colpate (8 colpi around equator and 4 on each apocolpium), small, 11  $\mu\text{m}$  long, , CEi 0.29, ends rounded, colpi marginate, margo produced by a gradual thinning of the columellae until they completely disappear and hence colpi are slightly sunken; tectate, exine 3  $\mu\text{m}$  thick, endexine 1  $\mu\text{m}$  thick, columellae 1  $\mu\text{m}$  thick, 1  $\mu\text{m}$  wide and 1  $\mu\text{m}$  apart, tectum 1  $\mu\text{m}$  thick; sculpture psilate to microechinate, microechinae only perceptible on cross section, very short 0.1-0.2  $\mu\text{m}$  tall; columellae tips seen through tectum giving the impression of a negative reticulum.

**Dimensions.** Equatorial diameter length 54-(56)-60  $\mu\text{m}$ , equatorial diameter width 50-(52)-54  $\mu\text{m}$ , length/width 1.07; nm=2, no=2.

**Remarks.** *Lymingtonia amazonica* sp. nov. is smaller and has 6 colpi. *Lymingtonia?* sp. 1 Jaramillo and Dilcher 2001 is intectate-echinate.

**Derivation of name.** After the latin word ‘splendens’ meaning shining or brilliant, for the pollen’s large size and exquisite morphology.

**Botanical affinity.** Convolvulaceae (*Evolvulus* spp., *Jacquemontia* spp.).

## Stephanocolpate

**Genus** *Retistephanocolpites* Leidekmeyer 1966

**Type species** *Retistephanocolpites angeli* Leidekmeyer 1966

*Retistephanocolpites curvimuratus* sp. nov.

Plate 23, figures 1-3

**Holotype.** Plate 23, figures 1-2, sample 22386, EF L-46-2

**Paratype.** Plate 23, figures 3, sample 22422, EF E-30

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular to quadrangular; stephanocolpate, 4 short colpi, 10  $\mu\text{m}$  long, CEi 0.27, CPi 0.25, borders slightly invaginated, ends pointed, costate, costa 3  $\mu\text{m}$  wide,  $\mu\text{m}$  thick; semitectate, exine 4  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$  thick, columellae 2  $\mu\text{m}$  long, distinct, 1  $\mu\text{m}$  thick, 0.5  $\mu\text{m}$  apart, tectum 1  $\mu\text{m}$  thick; reticulate, lumina 1.5-2  $\mu\text{m}$  wide, curvimate, muri 1  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Polar view: equatorial diameter length 42-(42.5)-43  $\mu\text{m}$ , equatorial diameter width 40-(41)-42  $\mu\text{m}$ , length/width 1.03. Equatorial view: polar diameter 40, equatorial diameter 44, polar/equatorial 0.9; nm=3, no=3.

**Remarks.** Curvimate stephanocolpate pollen have not been described yet. Similar to *Retistephanocolpites* sp. 2 Jaramillo and Dilcher 2001, but curvimate.

**Derivation of name.** After curvimate reticulum.

*Retistephanocolpites liberalis* sp. nov.

Plate 23, figures 4-6

**Holotype.** Plate 23, figures 4-5, sample 22282, EF L-14-2

**Paratype.** Plate 23, figures 6, sample 22287, EF S-17-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular to quadrangular; stephanocolpate, endo and ectocolpi coinciding, 4 colpi, simple, mid-sized, colpi 20  $\mu\text{m}$  long, CEi 0.54, borders slightly invaginated, ends pointed, colpi often wide open; tectate, exine 2  $\mu\text{m}$  thick, nexine 0.7  $\mu\text{m}$  thick, sometimes with endocracks, columellae 0.6  $\mu\text{m}$  long, distinct, ca. 0.5  $\mu\text{m}$  thick, 0.5  $\mu\text{m}$  apart, tectum 0.7  $\mu\text{m}$  thick; reticulate, lumina 1  $\mu\text{m}$  wide, rounded, elongate to angular, muri 1  $\mu\text{m}$  wide, homobrochate.

**Dimensions.** Equatorial diameter length 37-(37.5)-38  $\mu\text{m}$ , equatorial diameter width 33-(35)-37  $\mu\text{m}$ , length/width 1.07; nm=2, no=7.

**Remarks.** *Retistephanocolpites angeli* Leidekmeyer 1966 and *R. finalis* Gonzalez 1967 have 5 very short colpi. *R. regularis* van Hoeken-Klinkenberg 1966 has 5 longer colpi and smaller luminae. *R. tropicalis* Dueñas 1980 has minute lumina ( $< 0.5 \mu\text{m}$ ) and much more invaginated colpi. *R. circularis* Silva-Caminha *et al.* 2010 has 5 very short marginate colpi.

**Derivation of name.** After simple and open ('liberate') character of colpi.

*Retistephanocolpites passionis* sp. nov.

Plate 23, figures 7-9

**Holotype.** Plate 23, figures 7-8, sample 22261, EF H-38-3/4

**Paratype.** Plate 23, figures 9, sample 22272, EF G-6-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, spheroidal, circular amb; stephanocolpate, ecto and endocolpi coinciding, 6 colpi, simple, mid-sized, colpi  $14 \mu\text{m}$  long, CPi 0.46, CEi 0.55, borders straight, ends rounded, polar area  $8 \mu\text{m}$  wide; tectate, exine  $2.5 \mu\text{m}$  thick, nexine  $1 \mu\text{m}$  thick, columellae  $1 \mu\text{m}$  long, distinct,  $1 \mu\text{m}$  thick,  $2 \mu\text{m}$  apart, tectum  $0.5 \mu\text{m}$  thick; reticulate, lumina large,  $1\text{--}5 \mu\text{m}$  wide, rounded to angular, homobrochate, muri  $1 \mu\text{m}$  wide. Sporadic smaller luminae of ca.  $0.5 \mu\text{m}$  at the vertices of wider luminae; reticulum simplicolumellate, and exine within lumina is micropitted.

**Dimensions.** Equatorial view: polar diameter  $30 \mu\text{m}$ , equatorial diameter  $32 \mu\text{m}$ , polar/equatorial 0.93. Polar view: equatorial length  $36 \mu\text{m}$ , equatorial width  $30 \mu\text{m}$ , polar/equatorial 1.2; nm=2, no=4.

**Remarks.** *Retistephanocolpites angeli* Leidekmeyer 1966 and *R. finalis* Gonzalez 1967 have 5 very short colpi and have smaller luminae. *R. regularis* van Hoeken-Klinkenberg 1966 has 5 colpi and much smaller luminae. *R. tropicalis* Dueñas 1980 has minute lumina ( $< 0.5 \mu\text{m}$ ) and 4 colpi. *R. circularis* Silva-Caminha *et al.* 2010 has 5 very short marginate colpi.

**Derivation of name.** After affinity with *Passiflora* pollen.

**Botanical affinity.** *Passiflora* and Bignoniaceae (?).

### **Stephanocolporate**

*Loxocolporites foveolatus* gen. et sp. nov.

Plate 24, figures 1-3

**Holotype.** Plate 24, figures 1-1, sample 22140, EF J-40-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subprolate; staphanocolporate, loxocolporate, endo and ectocolpi coinciding, 4 colpori, colpi mid-sized, 12 µm long, CPi 0.63, borders straight, ends pointed, polar area 8 µm wide, ectocolpi simple, endocolpi costate, costa discrete, 1.5 µm wide, 1.5 µm thick; ectopores simple, lalongate, 4 x 3 µm wide; tectate, exine 1.5 µm thick, nexine 1 µm thick, columellae 0.3 µm thick, distinct, regularly distributed, very thin tectum, 0.2 µm thick. Ornamentation foveolate to micropitted foveolae circular, 0.5-1 µm wide, 0.5-1 µm apart, homobrochate.

**Dimensions.** Polar diameter 19 µm, equatorial diameter 16.5 µm, polar/equatorial 1.15; nm=1, no=1.

**Remarks.** This morphology had not yet been described in northern South America.

**Derivation of name.** Genus named from the term 'loxocolporate', and species after foveolate ornamentation.

**Genus** *Psilastephanocolporites* Leidelmeyer 1966

**Type species** *Psilastephanocolporites fissilis* Leidelmeyer 1966

*Psilastephanocolporites meliosus* sp. nov.

Plate 24, figures 7-8

**Holotype.** Plate 24, figures 7-8, sample 22140, EF L-22-1/3

**Paratype.** Plate 24, figures 9, sample 22140, EF X-32

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, subprolate to prolate; stephanocolporate, 5 colpi, endocolpi, mid-sized, colpi 16  $\mu\text{m}$  long, CPi 0.64, ends pointed, polar area rounded, 7  $\mu\text{m}$  wide, endocolpi costate, costa 1  $\mu\text{m}$  wide, 1.5  $\mu\text{m}$  thick; ectopores simple, circular, 5 x 5  $\mu\text{m}$ ; tectate, exine 2  $\mu\text{m}$  thick, nexine 1  $\mu\text{m}$  thick, sexine 1  $\mu\text{m}$  thick, columella absent, psilate.

**Dimensions.** Polar diameter 25-(28.16)-31.5  $\mu\text{m}$ , equatorial diameter 20-(21)-22  $\mu\text{m}$ , polar/equatorial 1.34; nm=2, no=74.

**Remarks.** *Psilastephanocolporites globulus* van Hoeken-Klinkenberg 1966 has 4 colpi, costate pores and is thicker. *P. marinamensis* Hoorn 1994 has 4 very short and indistinct colpi and lalongate pores. *P. matapiorum* Hoorn 1994 has 4 long colpi and lalongate pores. *P. schneideri* Hoorn 1993 has 4 colpi, large lalongate pores and is psilate-microreticulate. *Meliapollis* sp. 1 Silva-Caminha *et al.* 2010 has costate pores and simple colpi.

**Derivation of name.** After similarity with pollen from family Meliaceae (e.g. *Cedrela*).

**Botanical affinity.** Meliaceae (?).

*Psilastephanocolporites pseudomarinamensis* sp. nov.

Plate 24, figures 10-11

**Holotype.** Plate 24, figures 10-11, sample 22282, EF T-16-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, prolate spheroidal to subprolate, stephanocolporate, 5 colpi, endo and ectocolpi coinciding, mid-sized, colpi 16  $\mu\text{m}$  long, CPi 0.51, endocolpi costate, costa 2  $\mu\text{m}$  wide, 1.5  $\mu\text{m}$  thick, ends pointed, polar area rounded, 18  $\mu\text{m}$  wide;



ectopores simple, lalongate, 5 x 2  $\mu\text{m}$  wide, displaying a slight constriction, which makes them appear as 8-shaped; tectate, exine 2  $\mu\text{m}$  thick, nexine 0.7  $\mu\text{m}$  thick, columellae 0.6  $\mu\text{m}$  thick, indistinct, tectum 0.7  $\mu\text{m}$  thick. Psilate to micropitted, micropits < 0.5  $\mu\text{m}$ , evenly distributed and very short.

**Dimensions.** Polar diameter 23-(27)-31  $\mu\text{m}$ , equatorial diameter 22-(24)-26  $\mu\text{m}$ , polar/equatorial 1.12; nm=2, no=4.

**Remarks.** *Psilastephanocolporites marinamensis* Hoorn 1994 has shorter colpi, is psilate and pores are perfectly lalongate. *P. schneideri* Hoorn 1993 has much larger pores and is smaller.

**Derivation of name.** After an apparent similarity with *Psilastephanocolporites marinamensis* Hoorn 1994.

### Periporate

*Crotoperiporites pulcher* gen. et sp. nov.

Plate 24, figures 12-13

**Holotype.** Plate 24, figures 12-13, sample 22506, EF P-17

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; pantoporate, ecto/endopores coinciding, 12 pores, 2 x 2  $\mu\text{m}$  wide, circular, slightly costate, costa ca. 1  $\mu\text{m}$  wide; intectate, exine 2  $\mu\text{m}$  thick, nexine 0.5  $\mu\text{m}$  thick, sexine 1.5  $\mu\text{m}$  thick, composed of clavae; sculpture croton type, rosette formed of 6-7 triangular ornaments (clavae tips), total rosette width 3-4  $\mu\text{m}$  wide, circular to oval, adjoining the adjacent ones, with a circular centre of ca. 1  $\mu\text{m}$  wide, each triangular ornament is 1-1.5  $\mu\text{m}$  wide. Some grains display a reticulate pattern underneath clavae tips, probably formed by anastomosing clavae bases.

**Dimensions.** Equatorial diameter length 30-(32)-34  $\mu\text{m}$ ; equatorial diameter width 26-(27)-28  $\mu\text{m}$ , length/width 1.18; nm=2, no=3.

**Remarks.** The combination of periporate pollen with croton ornamentation had not been described before.

**Derivation of name.** The generic name *Crotoperiporites* derives from the ornamentation plus the apertures type, the specific name from the latin word ‘pulcher’ meaning beautiful.

**Genus** *Multiporopollenites* Thomson & Pflug 1953

**Type species** *Multiporopollenites maculosus* (Potonié 1931) Thomson & Pflug 1953

*Multiporopollenites intermedius* sp. nov.

Plate 25, figures 2-3

**Holotype.** Plate 25, figures 2-3, sample 22164, EF J-10-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; pantoporate, ecto/endopores coinciding, 14-16 pores, pores 3 x 3 µm wide, simple, circular; semitectate, exine 2 µm thick, nexine 1 µm thick, columellae 0.5 µm thick, distinct, < 0.5 µm wide, 0.5 µm apart, tectum 0.5 µm thick; reticulate, lumina 1 µm wide, elongate, muri 0.5-1 µm thick, homobrochate.

**Dimensions.** Equatorial diameter length 28 µm; equatorial diameter width 22-(23)-24 µm, length/width 1.21; nm=2, no=3.

**Remarks.** *Multiporopollenites crassinexinatus* Silva-Caminha *et al.* 2010 has 24 pores and a thicker nexine than sexine. *M. pauciporatus* Jaramillo and Dilcher 2001 has 18-23 pores and is micropitted.

**Derivation of name.** After its generalist/intermediate morphology.

**Genus** *Parsonsidites* Couper 1960

**Type species** *Parsonsidites psilatus* Couper 1960

*Parsonsidites? minibrenacii* sp. nov.

Plate 25, figures 5-6

**Holotype.** Plate 25, figures 5, sample 22518, EF E-43-4

**Paratype.** Plate 25, figures 6, sample 22506, EF R-6-1/2

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; pantoporate, ecto/endopores coinciding, 12-14 pores, pores 2 x 2  $\mu\text{m}$  wide, circular; tectate, exine 1  $\mu\text{m}$  thick, nexine 0.4  $\mu\text{m}$  thick, columellae 0.2  $\mu\text{m}$  thick, indistinct, tectum 0.4  $\mu\text{m}$  thick; psilate.

**Dimensions.** Equatorial diameter length 12-(12.6)-13  $\mu\text{m}$ ; equatorial diameter width 11-(11.6)-12  $\mu\text{m}$ , length/width 1.08; nm=3, no=85.

**Remarks.** *Paronsidites? brenacii* Silva-Caminha *et al.* 2010 is bigger and has relative thicker exine. *Multiporopollenites pauciporatus* Jaramillo and Dilcher 2001 is bigger, micropitted and has 18-23 pores.

**Derivation of name.** After resemblance with *P.? brenacii* Silva-Caminha *et al.* 2010, but much smaller size and thickness.

### **Genus** *Perisyncolporites* Germeraad *et al.* 1968

**Type species** *Perisyncolporites pokorny* Germeraad *et al.* 1968

*Perisyncolporites grossus* nov. sp.

Plate 25, figures 7-8

**Holotype.** Plate 25, figures 7-8, sample 22282, EF O-10

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; syncolporate, 8 pores (4 around equator and 1 in each pole), pores widen towards inner exine, from 3 to 4  $\mu\text{m}$  wide, circular, simple; endocolpi faintly developed and connecting one pore to the next adjacent pore, colpi 1.5  $\mu\text{m}$

wide; atectate, exine 4  $\mu\text{m}$  thick, psilate. Inner part of the exine at the poles can be thinner, creating an irregular circular mark.

**Dimensions.** Equatorial diameter length 32-(32.5)-33  $\mu\text{m}$ ; equatorial diameter width 30-(31.5)-33  $\mu\text{m}$ ; length/width 1.03; nm=2, no=2.

**Remarks.** *Perisyncolporites pokornyi* Germeraad *et al.* 1968 is thinner and tectate.

**Derivation of name.** After thick exine.

### **Genus** *Psilaperiporites* Regali 1974

**Type species** *Psilaperiporites robustus* Regali 1974

*Psilaperiporites pauciporatus* nov. sp.

Plate 25, figures 12-13

**Holotype.** Plate 25, figures 12-13, sample 22287, EF S-17-4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; pantoporate, endo and ectopores coinciding, pores 4 x 4  $\mu\text{m}$  wide, circular, simple, 5-6 pores; atectate, nexine 1  $\mu\text{m}$  thick, sexine 1.5  $\mu\text{m}$  thick, columellae absent; psilate.

**Dimensions.** Equatorial length 24  $\mu\text{m}$ ; equatorial width 22-(24)-26  $\mu\text{m}$ ; length/width 1; nm=2, no=6.

**Remarks.** *Psilaperiporites multiporatus* Hoorn 1994 is bigger and has 9-16 annulate pores.

*P. suarezi* Vajda-Santivanez 1999 has 16-34 pores. *P. brenacii* Silva-Caminha *et al.* 2010 is tectate and has 10 pores. *Parsonsidites?* sp. 1 Jaramillo and Dilcher 2001 has 9 pores arranged differently (3 in equator and 6 opposite to each other half-way equator-pole).

*Parsonsidites?* sp. 2 Jaramillo and Dilcher 2001 has 12 pores and is tectate.

*Multiporopollenites pauciporatus* Jaramillo and Dilcher 2001 is tectate and has 18-23 pores.

**Derivation of name.** After the low number of pores.

*Psilaperiporites redondus* nov. sp.

Plate 25, figures 14-15

**Holotype.** Plate 25, figures 14-15, sample 22349, EF J-11-1

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; pantoporate, ecto/endopores coinciding, pores 4 x 4 µm wide, circular, simple, 19-20 pores; tectate, exine 1 µm thick, nexine very thin, nearly absent, 0.2 µm thick, columella 0.4 µm thick, distinct, < 0.5 µm wide and < 0.5 µm apart, tectum 0.4 µm thick; psilate. Columellae tips clearly seen through tectum.

**Dimensions.** Equatorial diameter length 43 µm; equatorial diameter width 33 µm; equatorial diameter length/width 1.3; nm=1, no=2.

**Remarks.** *Psilaperiporites multiporatus* Hoorn 1994 and *P. suarezi* Vajda-Santibanez 1999 are atectate. *Parsonsidites? brenacii* Silva-Caminha *et al.* 2010, *P.? sp.* 1 Jaramillo and Dilcher 2001 and

*Parsonsidites? sp.* 2 Jaramillo and Dilcher 2001 have fewer spores. *Multiporopollenites pauciporatus* Jaramillo and Dilcher 2001 is micropitted and pores are relatively smaller in comparison to overall grain size.

**Derivation of name.** After rounded shape of pollen and pores.

### Stephanoporate

**Genus** *Verrustephanoporites* Leidekmeyer 1966

**Type species** *Verrustephanoporites simplex* Leidekmeyer 1966

*Verrustephanoporites dubius* sp. nov.

Plate 25, figures 18-19

**Holotype.** Plate 25, figures 18-19, sample 22412, EF M-13-2/4

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; stephanoporate, 6 pores, pores 2.5 x 2.5 µm wide, circular, costate, costa 1 µm wide and 1 µm thick; intectate, exine 2 µm thick, nexine 0.5 µm thick, sexine 1.5 µm thick; verrucate, verrucae circular to elongate, 2-4 µm wide, 0.5 µm apart, densely distributed over the entire surface.

**Dimensions.** Equatorial diameter length 26 µm; equatorial diameter width 24 µm; length/width 1.08; nm=1, no=3.

**Remarks.** *Verrustephanoporites intraverrucatus* sp. nov. has smooth sexine. *Ulmoideipites krempii* (Anderson, 1960) Elsik 1968 is tectate, has 3-5 pores and smaller verrucae.

**Derivation of name.** After false similarity with *Verrustephanoporites intraverrucatus* sp. nov. and *Ulmoideipites krempii* (Anderson, 1960) Elsik 1968

*Verrustephanoporites intraverrucosus* nov. sp.

Plate 25, figures 20-21

**Holotype.** Plate 25, figures 20-21, sample 22381, EF S-37-3

**Type locality:** Well 1-AS-105-AM, Solimões Formation, Amazonas, Brazil.

**Description.** Monad, radial, isopolar, circular; stephanoporate, 5 pores, pores 2 x 2 µm wide, circular, costate, costa 2 µm wide, formed of agglomeration of verrucae around pores, pores slightly protuding; atectate, exine 1.5 µm thick; infraverrucate, i.e. nexine is fragmented into verrucae, of circular shape, irregular size and distribution, 0.5-1 µm wide; verrucae of costae are larger.

**Dimensions.** Equatorial diameter length 30-(33.5)-37 µm, equatorial diameter width 28 µm; length/width 1.19; nm=2, no=3.

**Remarks.** *Ulmoideipites krempii* (Anderson, 1960) Elsik 1968 has external verrucae and is tectate.

**Derivation of name.** After internal verrucae.

**Botanical affinity.** *Forsteronia/Prestonia/Odontadenia* (Apocynaceae), but has even more resemblance with the African genus *Funtumia* (Apocynaceae).

Plate 1

- 1-2. *Echinosporis densiechinatus* sp. nov. (Holotype)
- 3-4. *Echinosporis densiechinatus* sp. nov. (Paratype)
5. *Laevigatosporites caoticus* sp. nov. (Holotype)
6. *Laevigatosporites caoticus* sp. nov. (Holotype)
7. *Laevigatosporites cultellus* sp. nov. (Holotype)
7. *Laevigatosporites cultellus* sp. nov. (Paratype)
9. *Laevigatosporites granulatus* Jaramillo *et al.* 2007
10. *Laevigatosporites tibuiensis* (Van der Hammen 1956a) Jaramillo and Dilcher 2001
11. *Microfoveolatosporis simplex* sp. nov.
12. *Polypodiisporites* aff. *speciosus*
13. *Polypodiisporites densus* sp. nov. (Holotype)
14. *Polypodiisporites densus* sp. nov. (Paratype)



# PLATE 1

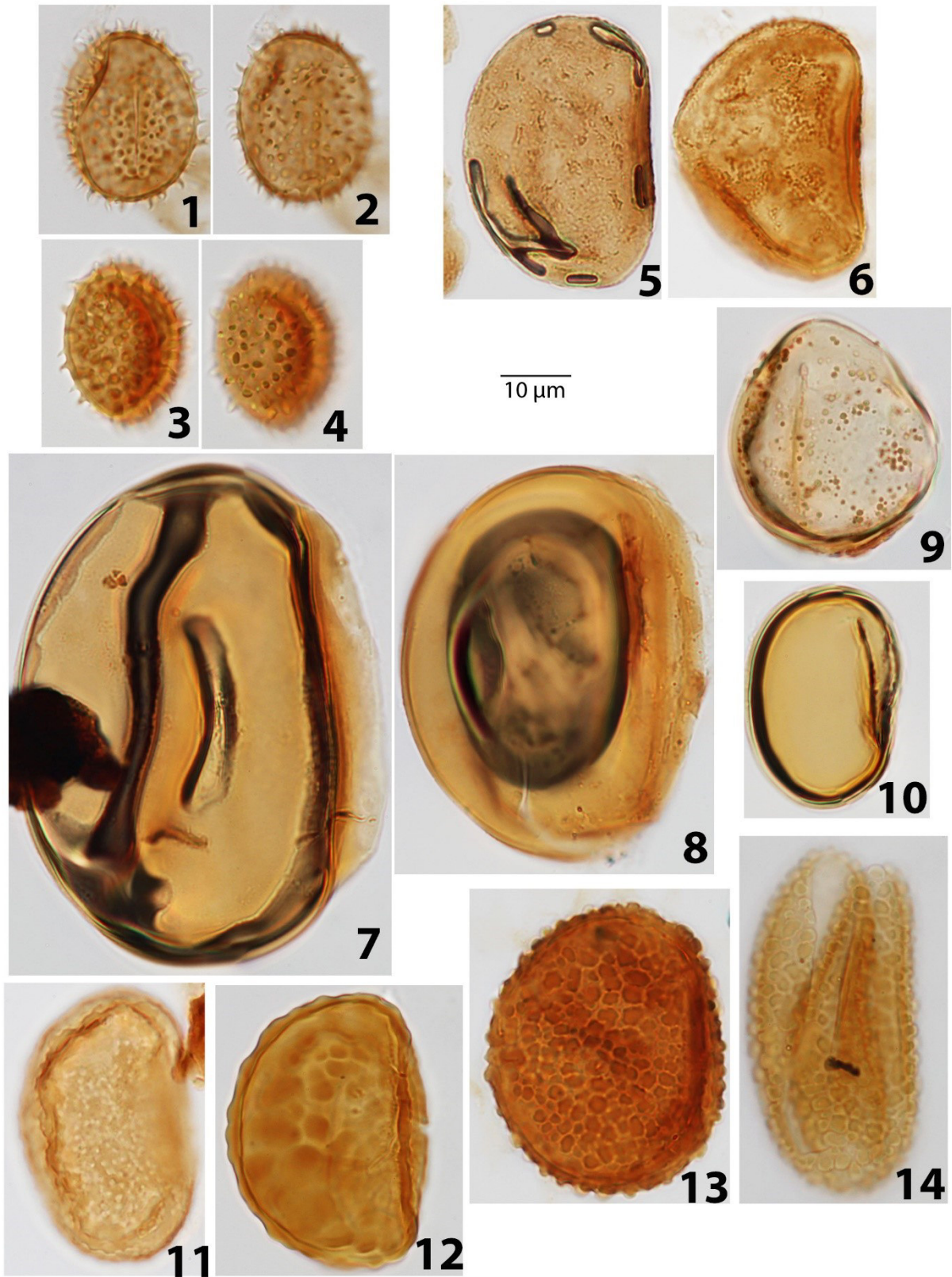


Plate 2

1. *Polypodiisporites discretus* sp. nov. (Holotype)
2. *Polypodiisporites discretus* sp. nov. (Paratype)
- 3-4. *Polypodiisporites fossulatus* sp. nov.
5. *Polypodiisporites scabraproximatus* Silva-Caminha *et al.* 2010
- 6-7. *Polypodiisporites usmensis* (Van der Hammen, 1956a) Khan and Martin 1972
8. *Polypodiisporites? planus* Silva-Caminha *et al.* 2010
- 9-10. *Punctatosporites? latrubessei* sp. nov. (Holotype)
- 11-12. *Punctatosporites? latrubessei* sp. nov. (Paratype)
- 13-14. *Reticulosporis diversus* sp. nov. (Holotype)
- 15-16. *Reticulosporis diversus* sp. nov. (Paratype)

**Plate 2**

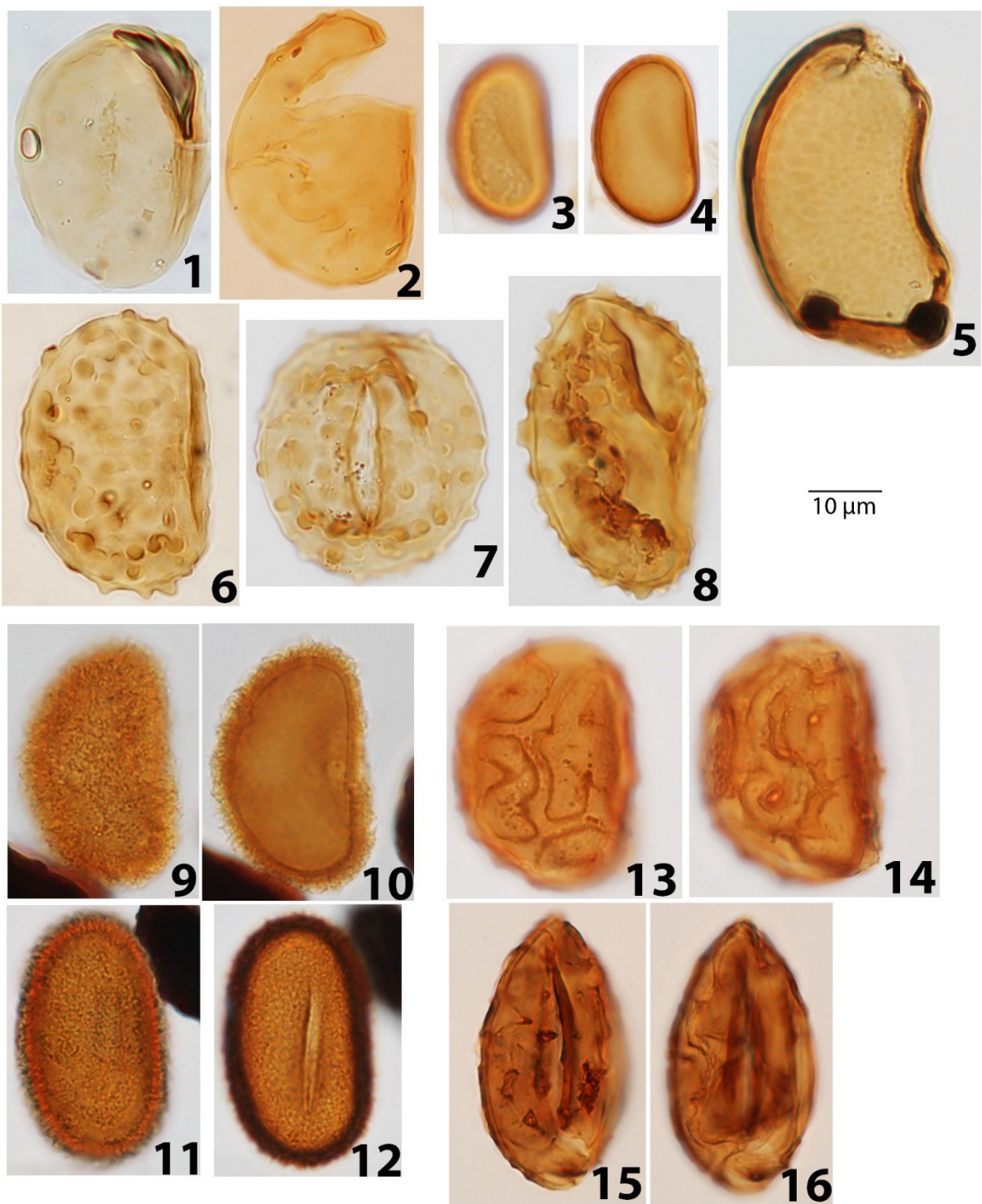


Plate 3

1\*. *Azolla* sp.

2-3. *Camarozonosporites crassus* Silva-Caminha *et al.* 2010

4-5. *Camarozonosporites fossulatus* sp. nov.

6-7. *Camarozonosporites trilobatus* sp. nov. (Holotype)

8-9. *Camarozonosporites trilobatus* sp. nov. (Holotype)

10-11. *Cicatricosisporites baculatus* Regali *et al.* 1974

12-13\*. *Cicatricosisporites pseudograndiosus* sp. nov.

14. *Cingulatisporites cristatus* sp. nov.

15-16. *Cingulatisporites matisiense* sp. nov. (Holotype)

17-18. *Cingulatisporites matisiense* sp. nov. (Paratype)

\*picture is half sized



# Plate 3

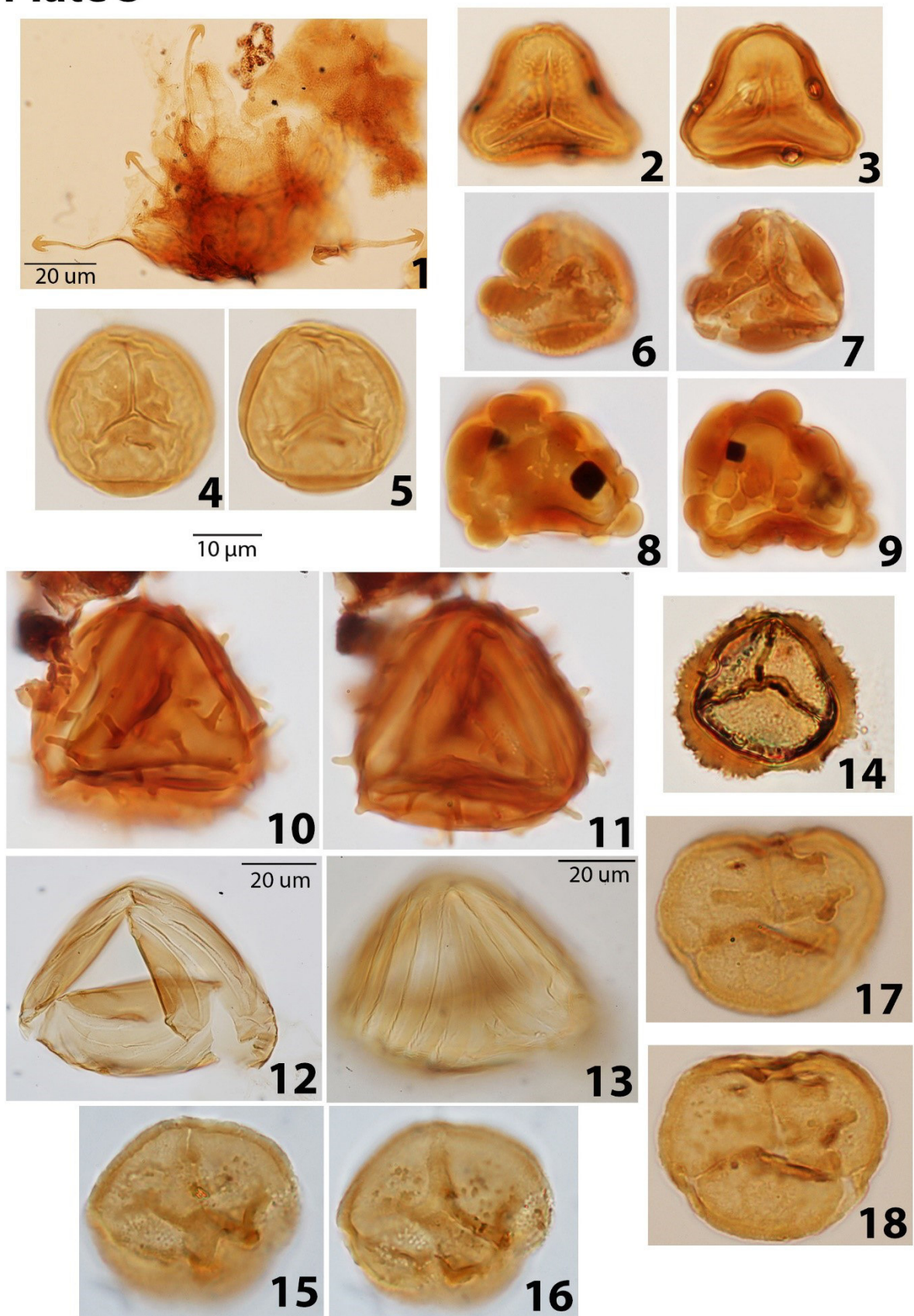


Plate 4

1-2\*. *Crassoretitriletes vanraadshoovenii* Germeraad *et al.* 1968

3\*. *Deltaidospora adriennis* (Potonié and Gelletich 1933) Frederiksen 1983

4-5. *Distaverrusporites margaritatusi* Muller 1968

6. *Echinatisporis circularis* Silva-Caminha *et al.* 2010

7-8. *Echinatisporis connectus* sp. nov. (Holotype)

9-10. *Echinatisporis connectus* sp. nov. (Paratype)

11-12. *Echinatisporis infantus* sp. nov. (Holotype)

13. *Echinatisporis infantus* sp. nov. (Paratype)

\*picture is half sized

**Plate 4**

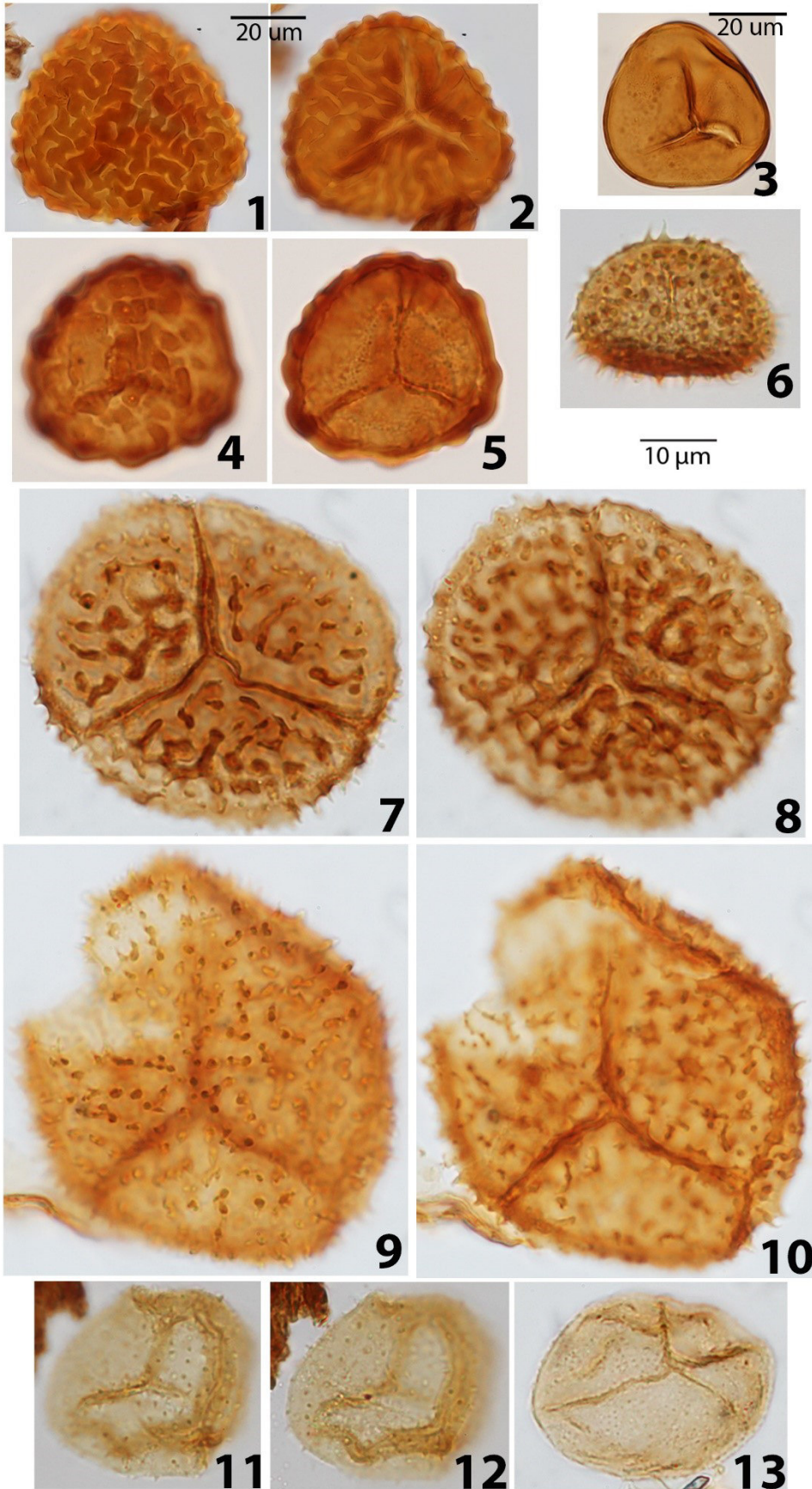




Plate 5

1. *Echinatisporis muelleri* (Regali *et al.* 1974) Silva-Caminha *et al.* 2010

2-3. *Foveotriletes ornatus* Regali *et al.* 1974

4-5. *Hamulatisporis bare* sp. nov.

6-7. *Hydrosporis minor* Silva-Caminha *et al.* 2010

8-9. *Ischyosporites dubius* sp. nov. (Holotype)

10-11. *Ischyosporites dubius* sp. nov. (Paratype)

12-13. *Ischyosporites granulatus* sp. nov.

14. *Kuylisporites waterbolkii* Potonié 1956

15-16. *Lycopodiumsporites clavatooides* sp. nov.



# Plate 5

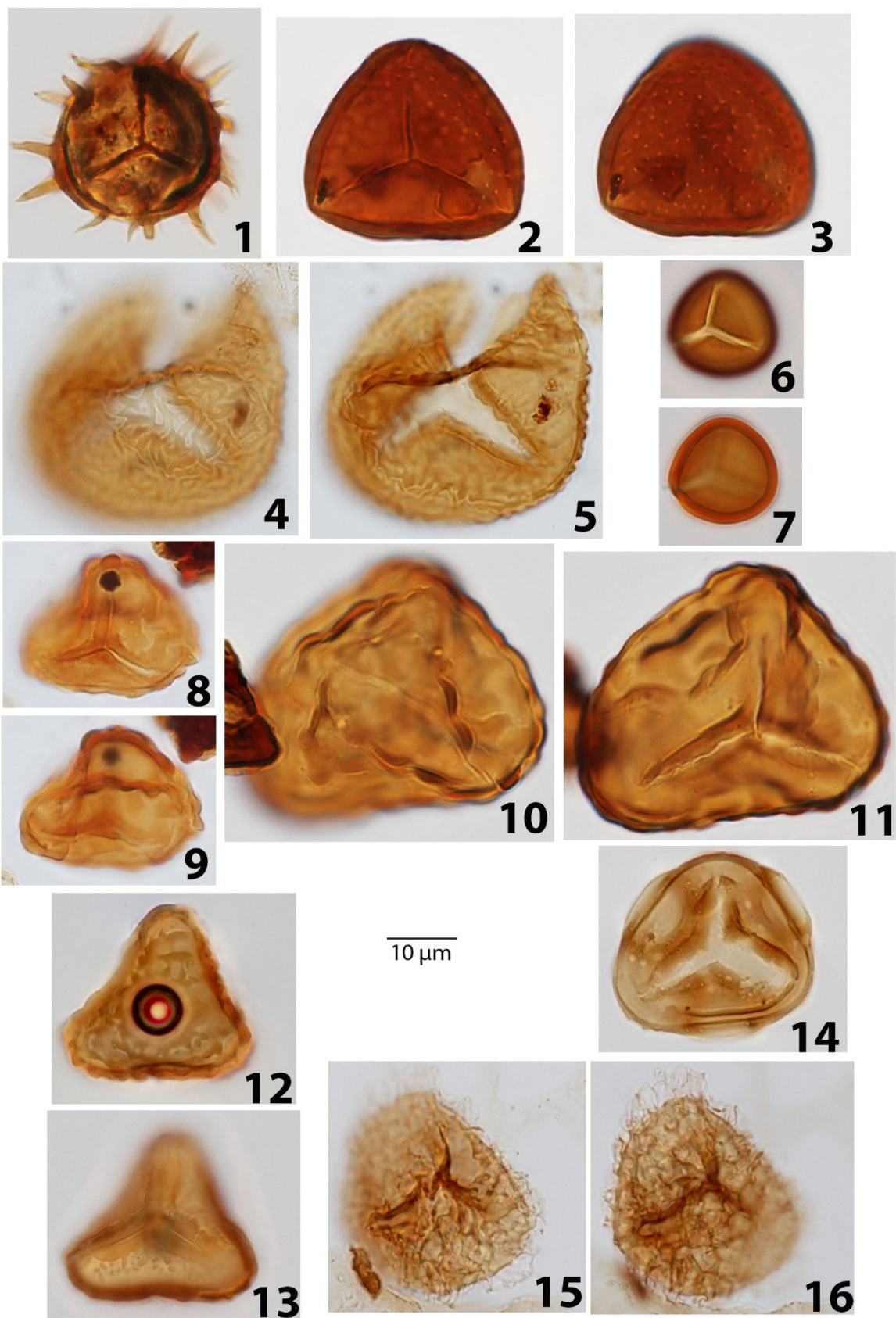


Plate 6

1. *Magnastriatites grandiosus* (Kedves and Sole de Porta 1963) Dueñas 1980

2-3. *Neoraistrickia dubiosa* sp. nov. (Holotype)

4-5. *Neoraistrickia dubiosa* sp. nov. (Paratype)

6-7. *Nijssenosporites fossulatus* Lorente 1986

8-9. *Polypodiaceoisporites pseudopsilatus* Lorente 1986

10. *Psilatriletes delicatus* sp. nov. (Holotype)

11. *Psilatriletes delicatus* sp. nov. (Paratype)

12. *Psilatriletes lobatus* Hoorn 1994

13-14. *Psilatriletes marginata* (Holotype)

15. *Psilatriletes marginata* (Paratype)

# Plate 6

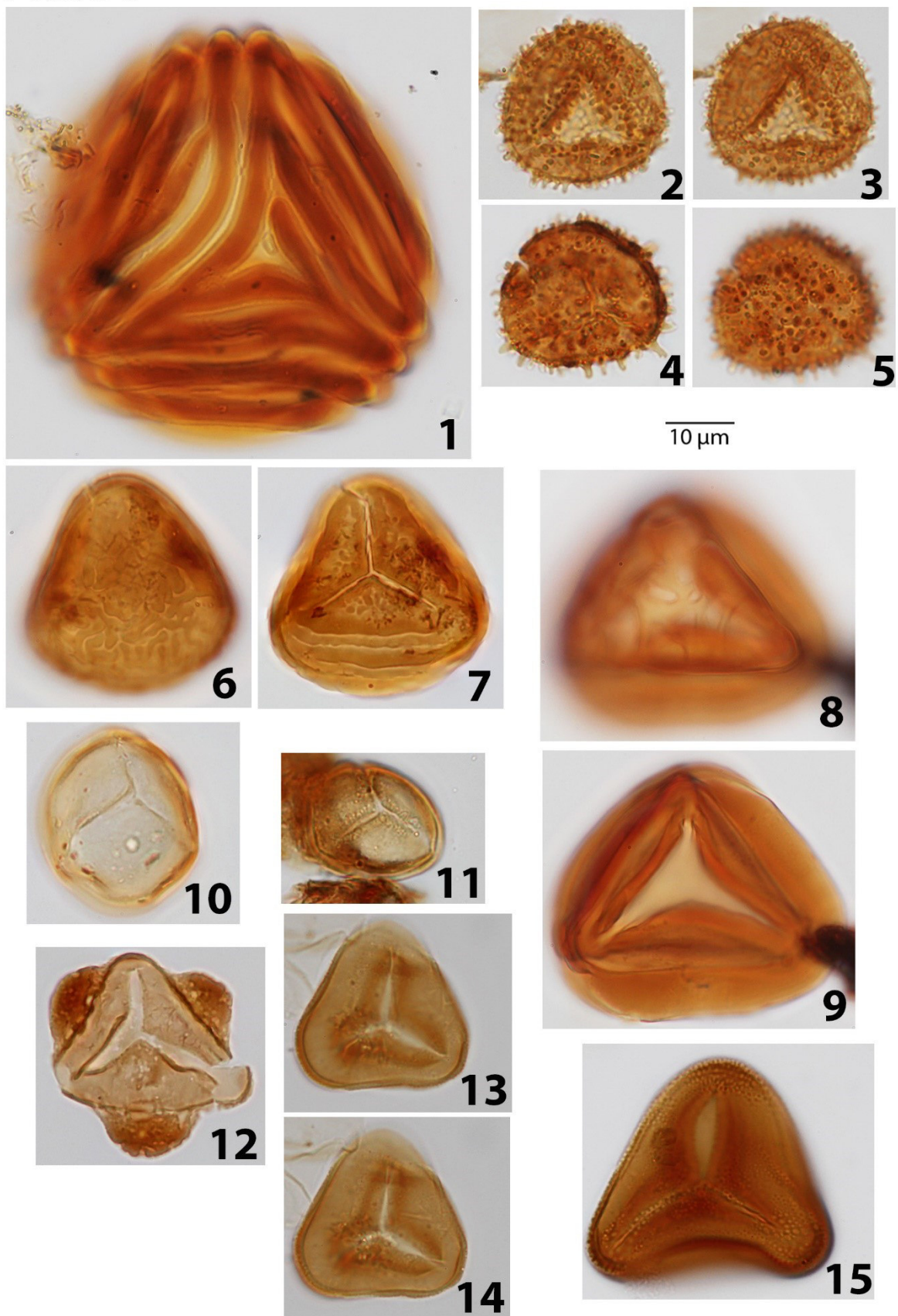


Plate 7

1-2. *Pteridaceoisporis gemmatus* Silva-Caminha *et al.* 2010

3-4. *Retitriletes altimuratus* Silva-Caminha *et al.* 2010

5-6. *Rotverrusporites amazonicus* sp. nov. (Holotype)

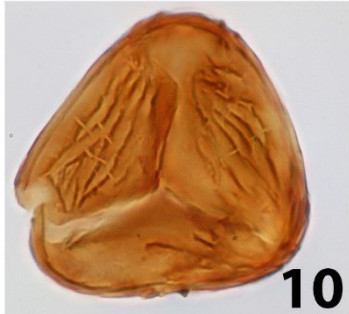
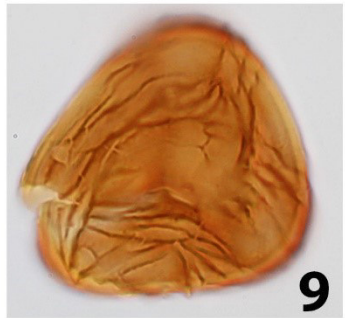
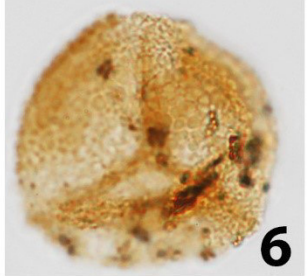
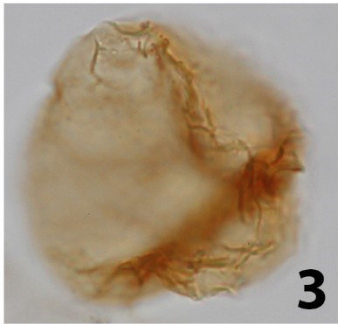
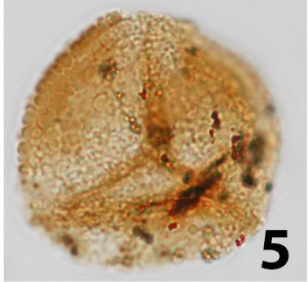
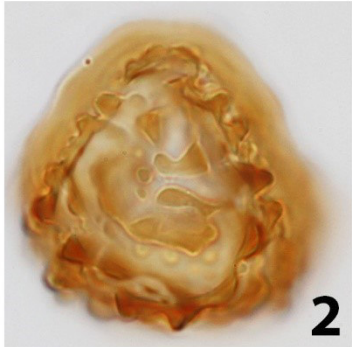
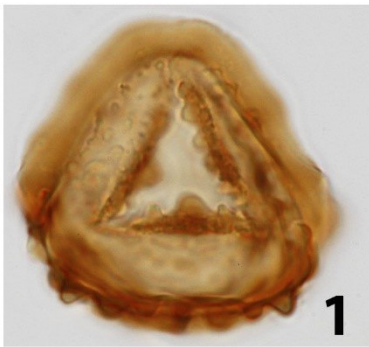
7-8. *Rotverrusporites amazonicus* sp. nov. (Paratype)

9-10. *Striatriletes saccolomoides* Jaramillo *et al.* 2010

11-12. *Verrucatotriletes pseusoviruleoides* sp. nov.



**Plate 7**



10  $\mu\text{m}$

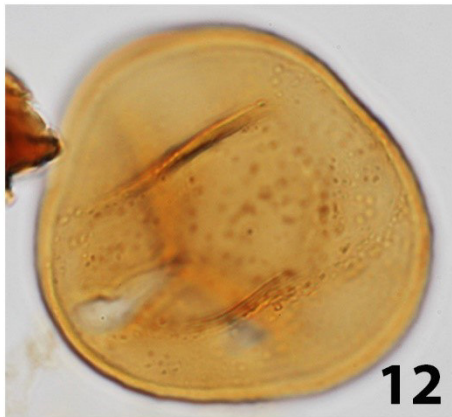


Plate 8

1. *Clavainaperturites microclavatus* Hoorn 1994
- 2-3\*. *Crotonoidaepollenites reticulatus* Silva-Caminha *et al.* 2010
4. *Inaperturopollenites tectatus* sp. nov.
- 5-8. *Polyadopollenites macroreticulatus* Salard-Chebouldaeff 1974
9. *Polyadopollenites mariae* Dueñas 1980
10. *Arecipites membranosus* sp. nov.
11. *Arecipites perfectus* Silva-Caminha *et al.* 2010
12. *Arecipites regio* (Van der Hammen and Garcia, 1966) Jaramillo and Dilcher, 2001
- 13-14. *Clavamonocolpites lorentei* Muller *et al.* 1987
15. *Longapertites lisus* sp. nov. (Holotype)
16. *Longapertites lisus* sp. nov. (Paratype)
17. *Longapertites microfoveolatus* Adegoke and Jan du Chene 1975

\*picture 3 was taken with phase contrast

## Plate 8

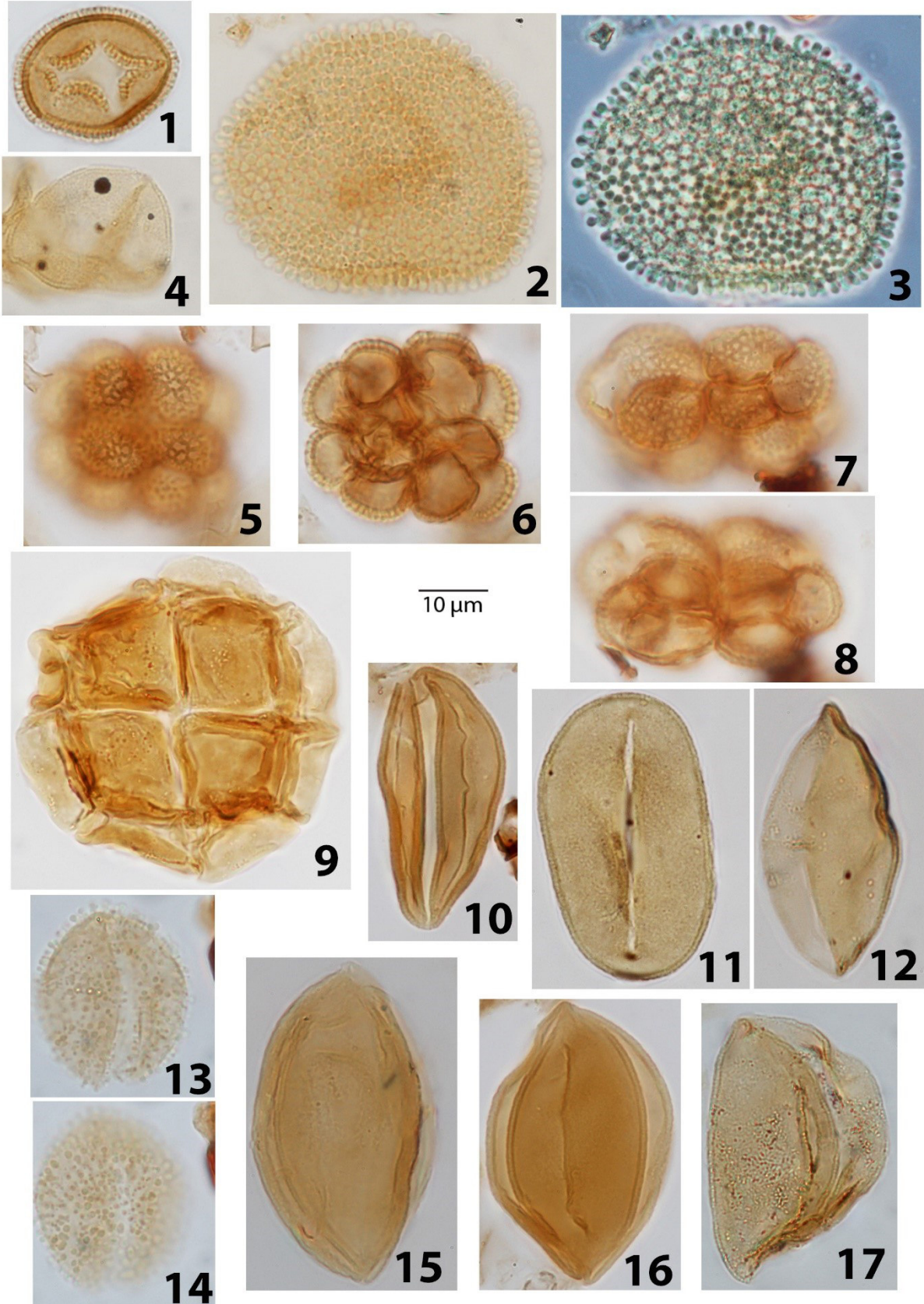




Plate 9

1-2. *Longapertites sutilis* sp. nov.

3-4. *Mauritiidites franciscoi* var. *franciscoi* (Van der Hammen, 1956) Van Hoeken Klinkenberg 1964

5. *Mauritiidites franciscoi* var. *minutus* Van der Hammen and Garcia 1966

6. *Mauritiidites franciscoi* var. *pachyexinatus* Van der Hammen and Garcia 1966

7. *Psilamonocolpites amazonicus* Hoorn 1993

8. *Psilamonocolpites medius* (Van der Hammen, 1956) Van der Hammen and Garcia, 1966

9. *Psilamonocolpites nanus* Hoorn 1993

10. *Retimonocolpites absyae* Hoorn 1993

11-12. *Retimonocolpites normalis* sp. nov.

13-14\*. *Proxapertites finus* sp. nov.

15. *Proxapertites psilatus* Sarmiento 1992

16\*. *Proxapertites tertiaria* Van der Hammen and Garcia 1966

17. *Trichotomosulcites amazonicus* sp. nov.

18. *Trichotomosulcites normalis* sp. nov.

\*picture is half sized



# Plate 9

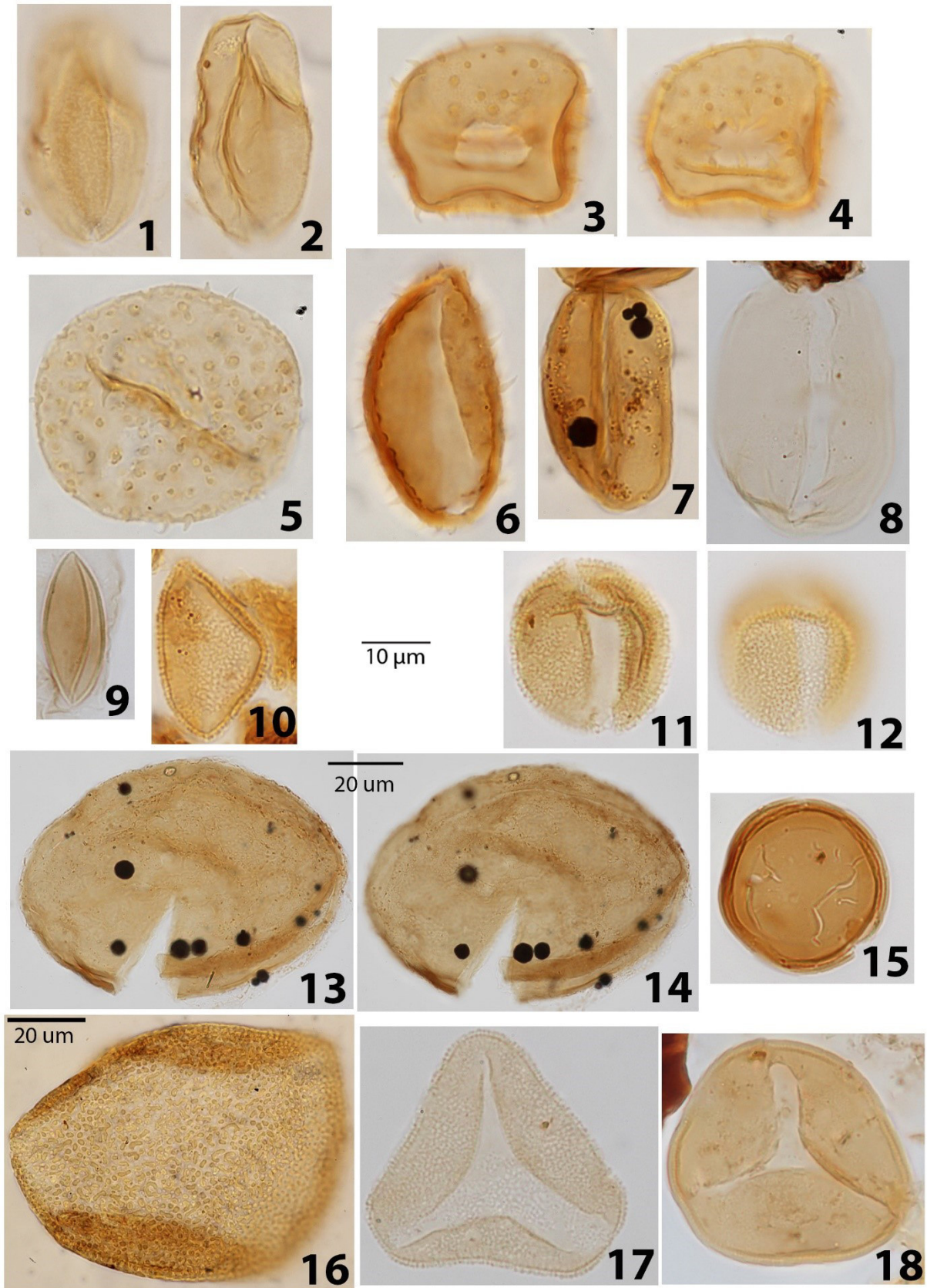


Plate 10

1. *Monoporopollenites annulatus* (Van der Hammen, 1954) Jaramillo and Dilcher 2001

2-3. *Monoporopollenites annuloides* sp. nov.

4-5. *Dicolpopollis? costatus* sp. nov.

6. *Multimarginites vanderhammenii* Germeraad *et al.* 1968

7. *Cyclusphaera scabrata* Jaramillo and Dilcher 2001

8-10. *Echidiporites barbeitoensis* Muller *et al.* 1987

11. *Psiladiporites minimus* Van der Hammen and Wymstra 1964

12. *Psiladiporites redundantis* Gonzalez 1967

13-14. *Crassiectoapertites columbianus* (Dueñas 1980) Lorente 1986

15. *Crototricolpites annemaria* Leidelmeyer 1966

16. *Crototricolpites finitus* Silva-Caminha *et al.* 2010

17-18. *Foveotricolpites colpiconstrictus* Hoorn 1994 nov. comb.

# Plate 10

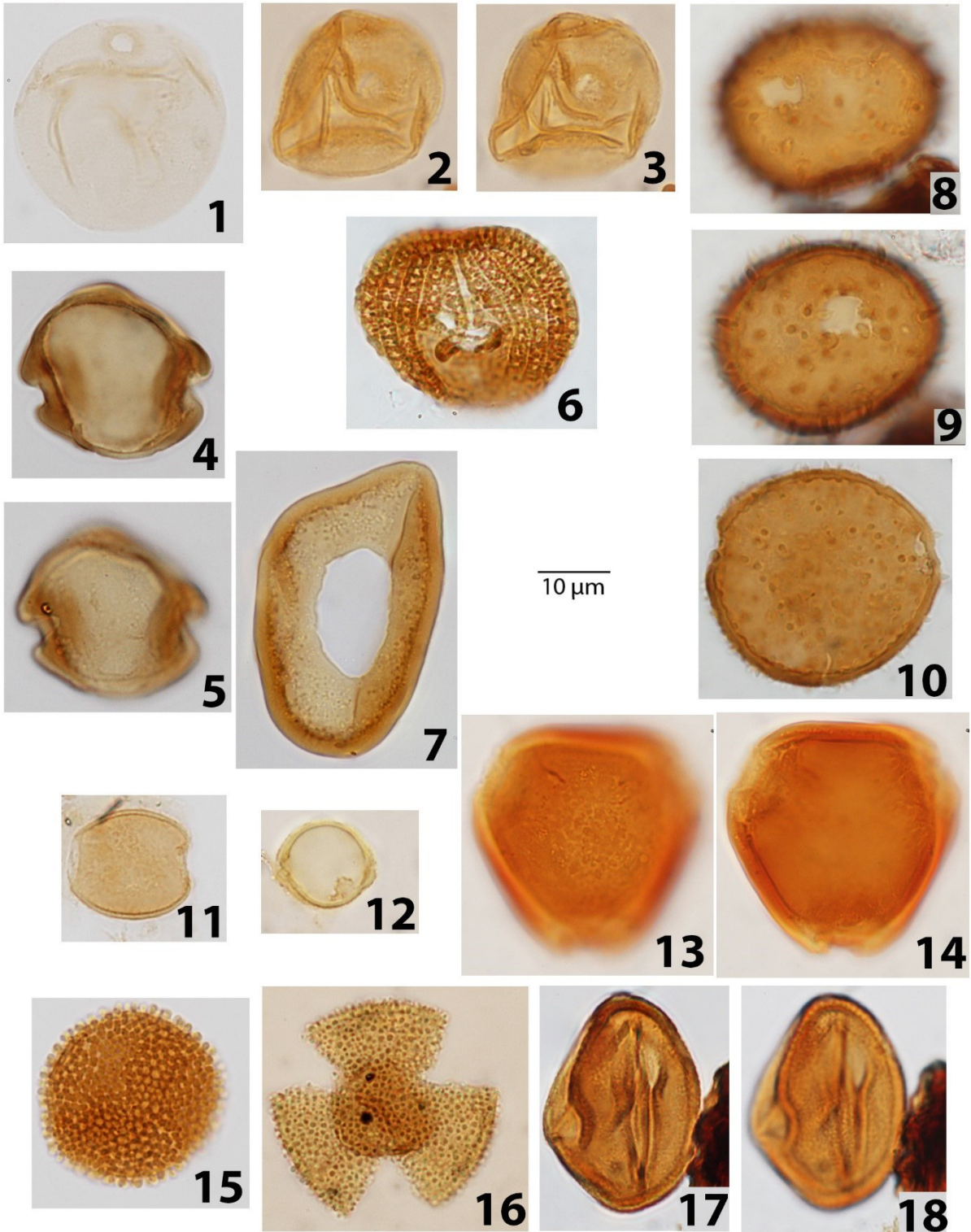


Plate 11

1-3. *Foveotricolpites simplex* Gonzalez 1967 nov. comb.

4-5. *Ladakhipollenites baitacolumellatus* sp. nov. (Holotype)

6. *Ladakhipollenites baitacolumellatus* sp. nov. (Paratype)

7-8. *Ladakhipollenites colpiconstrictus* van Hoeken-Klinkenberg 1966 nov. comb.

9-10. *Ladakhipollenites nanus* sp. nov.

11-12. *Ladakhipollenites simplissimus* sp. nov.

13-14. *Perfotricolpites digitatus* Gonzalez 1967



## Plate 11

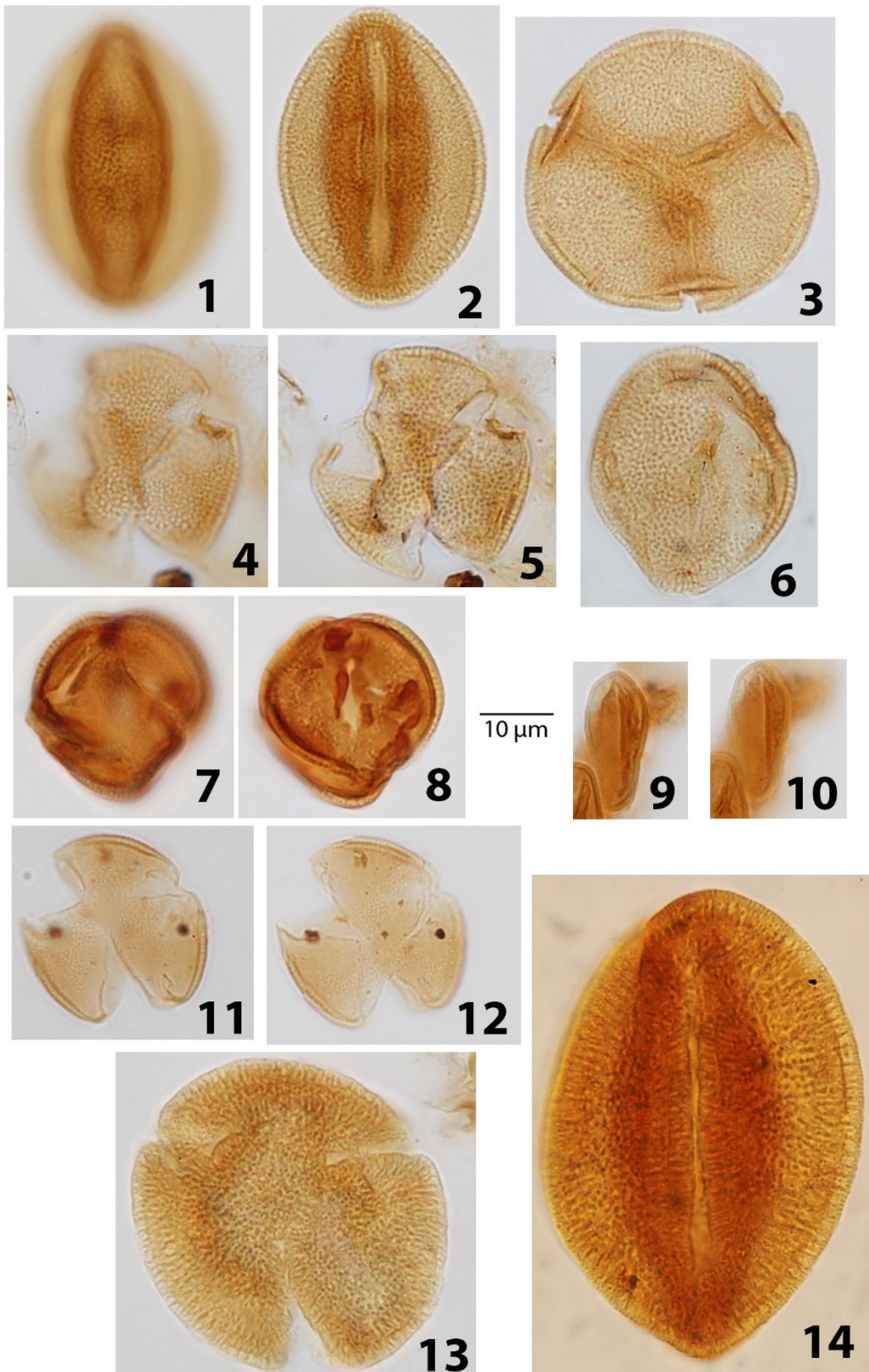


Plate 12

1. *Retibrevitricolpites pseudoretibolus* sp. nov. (Holotype)
2. *Retibrevitricolpites pseudoretibolus* sp. nov. (Paratype)
3. *Retitrescolpites brevicolpatus* sp. nov.
4. *Retitrescolpites magnus* (Gonzalez 1967) Jaramillo and Dilcher 2001
- 5-6. *Rhoipites? colpiverrucosus* sp. nov.
- 7-8. *Rhoipites? pluricolumellatus* nov. sp.
- 9-10. *Spirosyncolpites spiralis* Gonzalez 1967
11. *Tricolpites? pseudoclarensis* Silva-Caminha *et al.* 2010
12. *Bombacacidites araracuarensis* Hoorn 1994
13. *Bombacacidites baculatus* Muller *et al.* 1987
14. *Bombacacidites brevis* (Dueñas 1980) Muller *et al.* 1987

## Plate 12

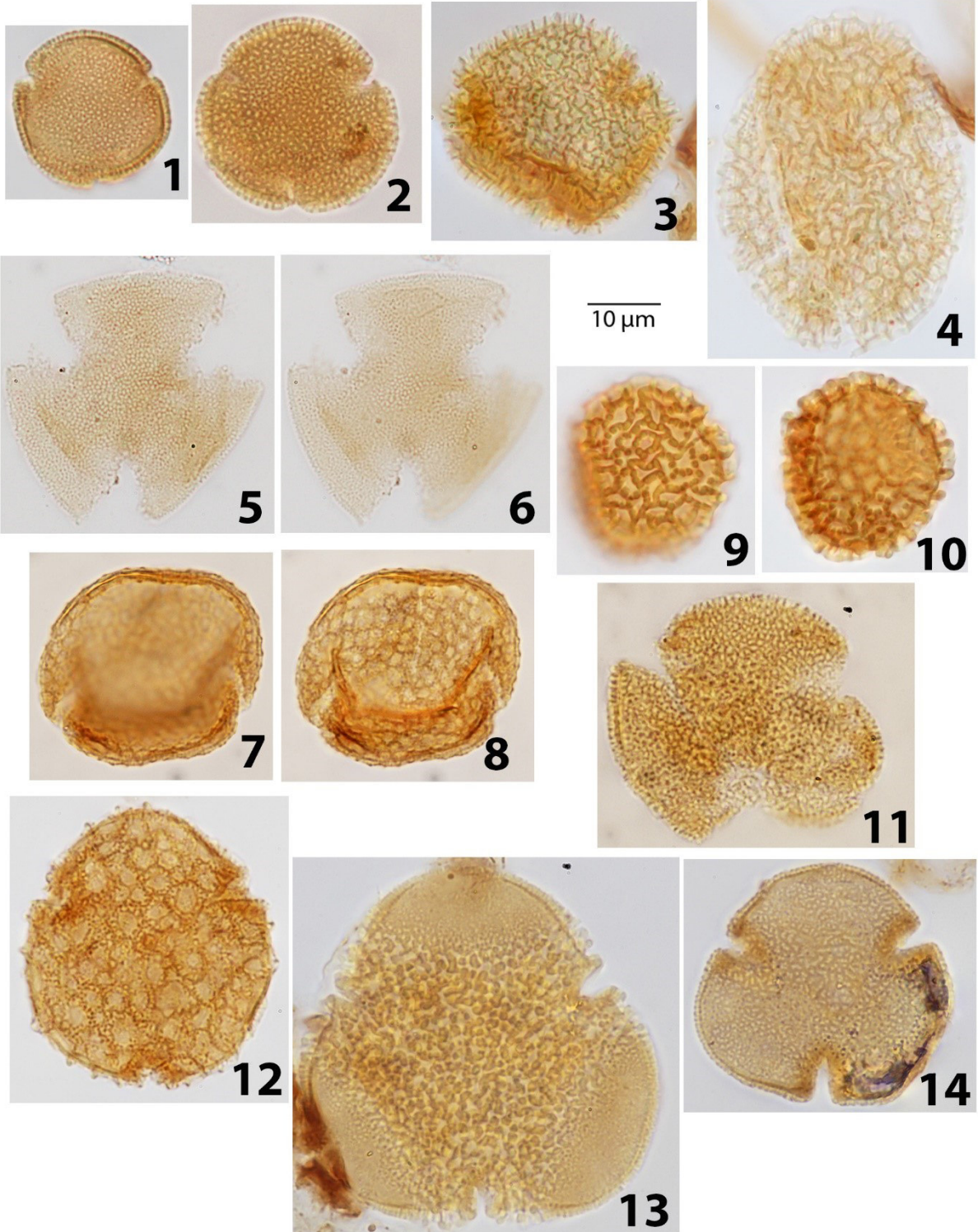




Plate 13

- 1-2. *Bombacacidites germeraadi* sp. nov.
3. *Bombacacidites lorentae* Hoorn 1993 nov. comb.
4. *Bombacacidites muinaneorum* Hoorn 1993
5. *Bombacacidites nacimientoensis* (Anderson 1960) Elsik 1968
6. *Cichoreacidites longispinosus* (Lorente 1986) Silva-Caminha *et al.* 2010
- 7-8. *Echitricolporites magnificus* sp. nov. (Holotype)
- 9-10. *Echitricolporites magnificus* sp. nov. (Paratype)
- 11-12. *Echitricolporites mcneillyi* Germeraad *et al.* 1968
- 13-14. *Echitricolporites spinosus* Van der Hammen 1956
- 15-16. *Ericipites annulatus* Gonzalez 1967



## Plate 13

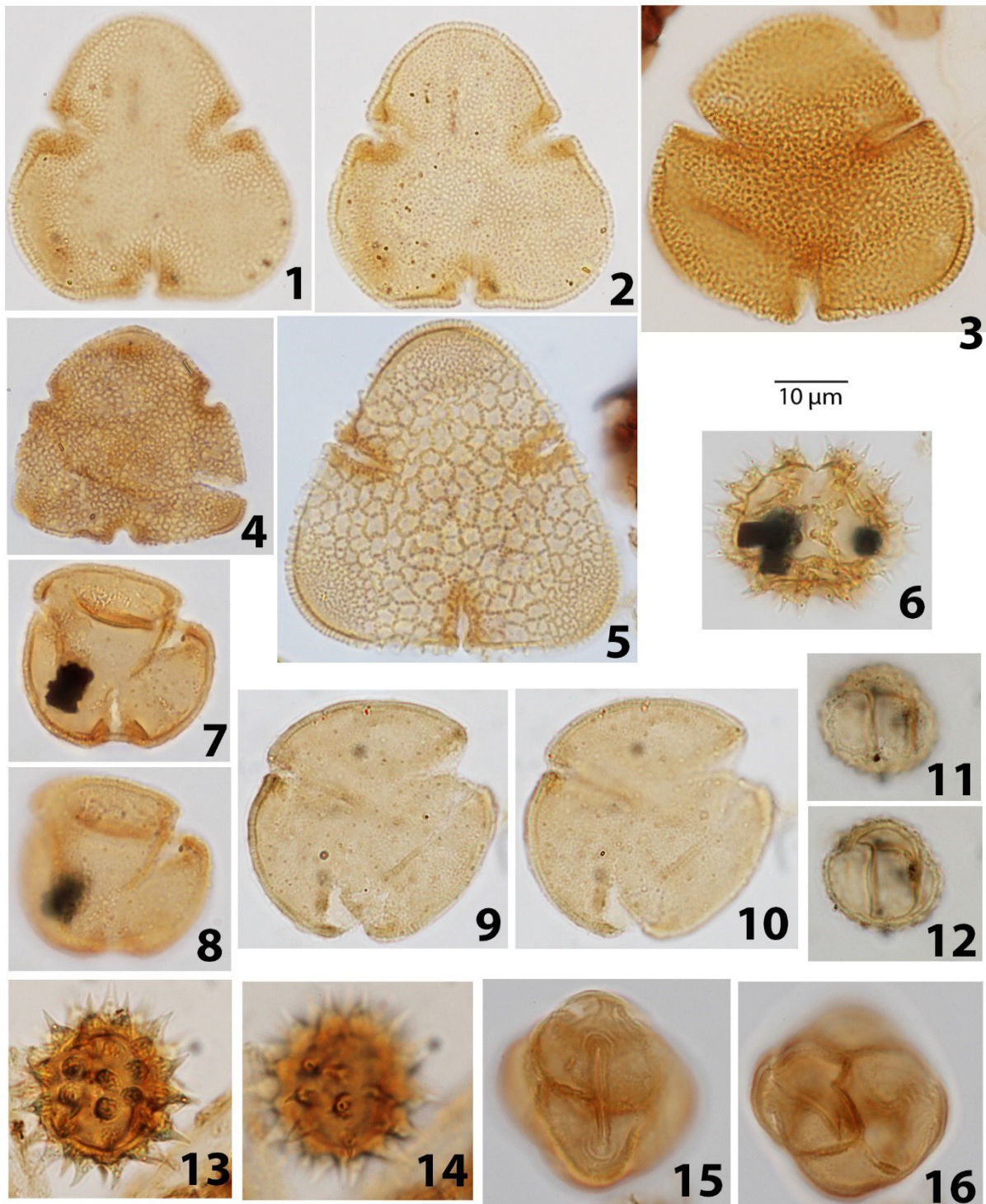


Plate 14

1. *Fenestrites spinosus* Van der Hammen 1956
- 2-3. *Foveotricolporites lolongatis* sp. nov.
4. *Foveotricolporites pseudodubiosus* Silva-Caminha *et al.* 2010
- 5-6. *Ilexipollenites tropicallis* Silva-Caminha *et al.* 2010
7. *Ladakhipollenites? Caribbiensis* (Muller *et al.* 1987) Silva-Caminha *et al.* 2010
8. *Ladakhipollenites? cassioides* (Holotype)
- 9-10. *Ladakhipollenites? cassioides* (Paratype)
- 11-12. *Ladakhipollenites? corvattatus* sp. nov.
- 13-14. *Ladakhipollenites? endoporatus* sp. nov.
- 15-17. *Ladakhipollenites? garzonni* Hoorn 1993 nov. comb.
18. *Ladakhipollenites? labiatus* Hoorn 1993 nov. comb.
- 19-20. *Ladakhipollenites? magniporatus* Hoorn 1993 nov. comb.
21. *Ladakhipollenites? nanus* sp. nov.
- 22-23. *Ladakhipollenites? obesus* Hoorn 1993 nov. comb.
24. *Ladakhipollenites? pseudonanus* sp. nov.
- 25-26. *Ladakhipollenites? pseudosilvaticus* sp. nov.
- 27-28. *Ladakhipollenites? silvaticus* Hoorn 1993 nov. comb.
- 29-30. *Ladakhipollenites? sphericus* sp. nov.



# Plate 14

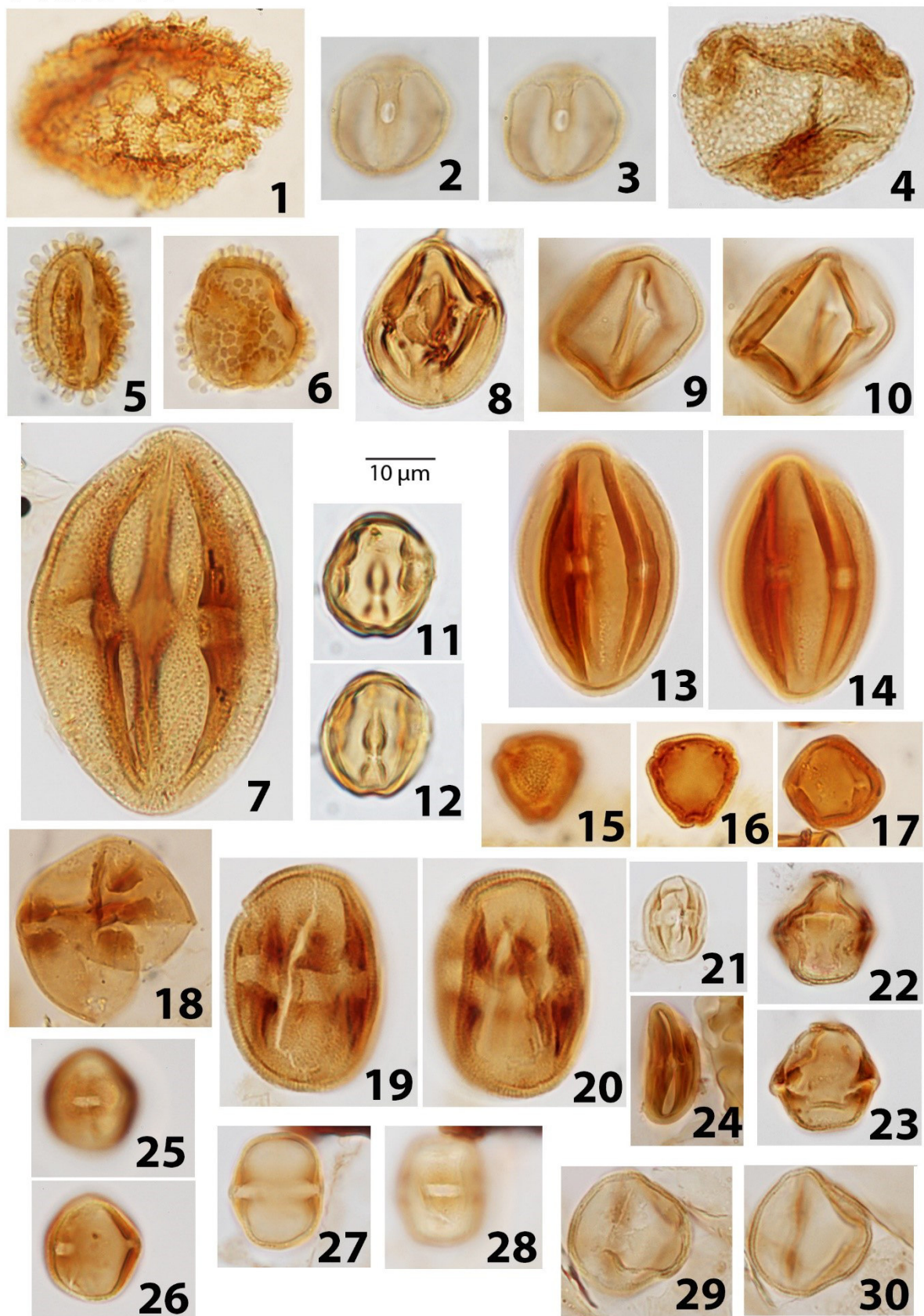


Plate 15

1-3. *Ladakhipollenites? xatanawensis* sp. nov. (Holotype)

4. *Ladakhipollenites? xatanawensis* sp. nov. (Paratype)

5-6. *Lakhiapollis costatus* Silva-Caminha *et al.* 2010

7-8. *Lanagiopollis crassa* (Van der Hammen and Wymstra 1964) Frederiksen 1988

9-10. *Malvacipolloides dubiosus* sp. nov.

11-12. *Malvacipolloides maristellae* (Muller *et al.* 1987) Silva-Caminha *et al.* 2010

13-15. *Margocolporites bilinearis* sp. nov.

16-17. *Margocolporites carinae* sp. nov.

18-19. *Margocolporites* “*incertus*”



# Plate 15

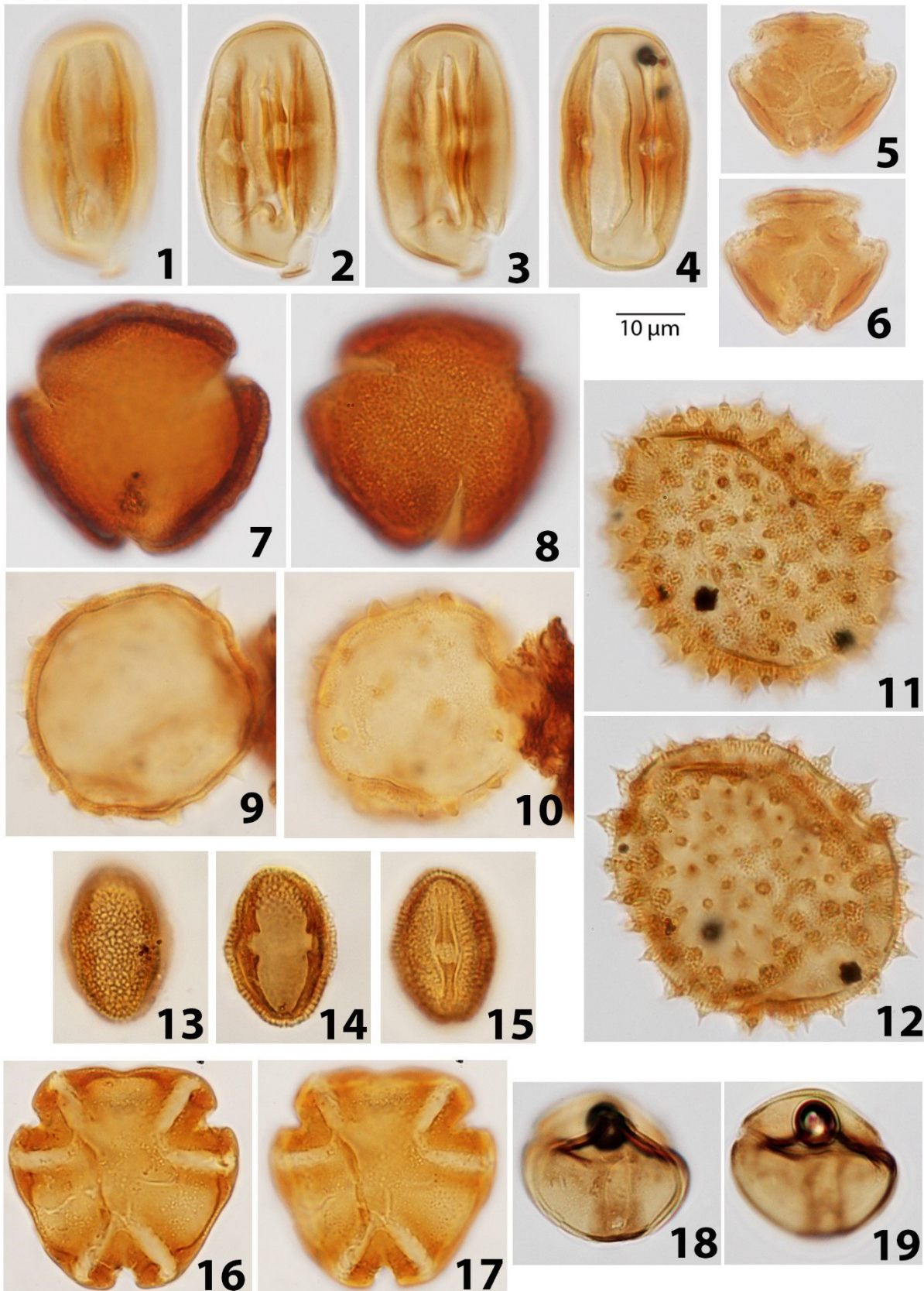


Plate 16

1-2. *Margocolporites vanwijhei* Germeraad *et al.* 1968

3-4. *Paleosantaceaepites* cf. *cingulatus*

5-6. *Paleosantaceaepites invaginatus* sp. nov.

7-8. *Paleosantalaceaepites kaarsii* Hoorn 1993 nov. comb.

9-11. *Psilabrevitricolporites devriesii* (Lorente 1986) Silva-Caminha *et al.* 2010

12-13. *Psilabrevitricolporites triangularis* (Van der Hammen and Wymstra 1964) Jaramillo and Dilcher 2001

14. *Ranunculacidites operculatus* (Van der Hammen and Wymstra 1964) Jaramillo and Dilcher 2001

15-16. *Ranunculacidites reticulatus* sp. nov. (Holotype)

17. *Ranunculacidites reticulatus* sp. nov. (Paratype)

18-19. *Retibrevitricolporites retibolus* Leidelmeyer 1966

20-23. *Retibrevitricolporites solimoensis* Hoorn 1993 nov. comb.

24-25. *Retibrevitricolporites yavarensis* (Hoorn 1993) Silva-Caminha *et al.* 2010



# Plate 16

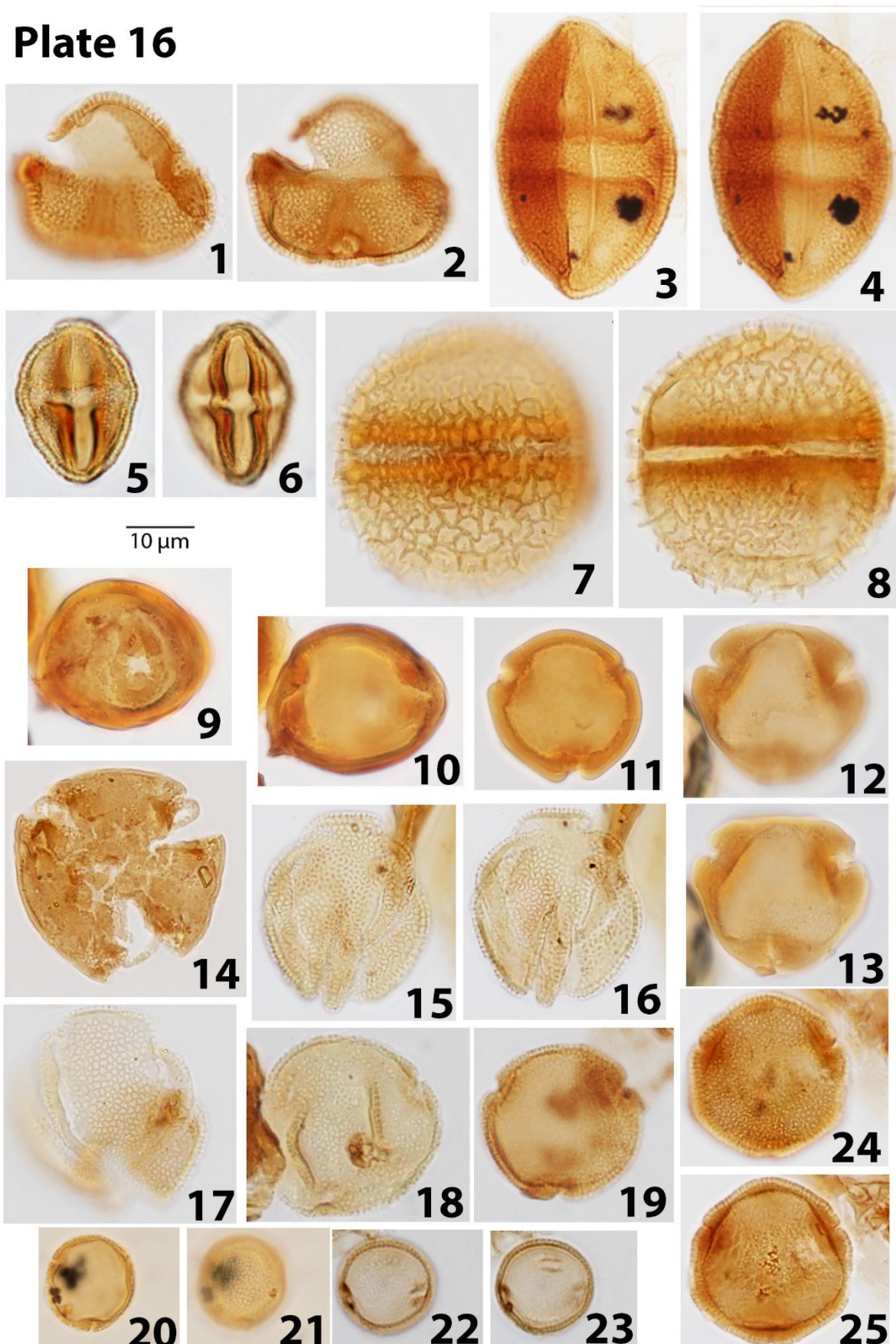


Plate 17

1-2. *Retitrescolpites benjaminense* sp. nov. (Holotype)

3-4. *Retitrescolpites benjaminense* sp. nov. (Paratype)

5-6. *Retitrescolpites grossus* sp. nov.

7-9. *Retitrescolpites marginatus* sp. nov.

10-11. *Retitrescolpites? Irregularis* (Van der Hammen and Wymstra 1964) Jaramillo and Dilcher  
2001

12-13. *Retitrescolpites? Traversei* Silva-Caminha *et al.* 2010

14-15. *Retitricolporites milnei* Hoorn 1993

16-17. *Retitricolporites ticoneorum* Hoorn 1993

18-19. *Rhoipites caputoi* Hoorn 1993 nov. comb.

20-21. *Rhoipites caricatus* sp. nov. (Holotype)

22-23. *Rhoipites caricatus* sp. nov. (Paratype)

24-25. *Rhoipites crassicostatus* Van der Hammen and Wymstra 1964 nov. comb.

26-27. *Rhoipites crassitectatus* sp. nov.



# Plate 17

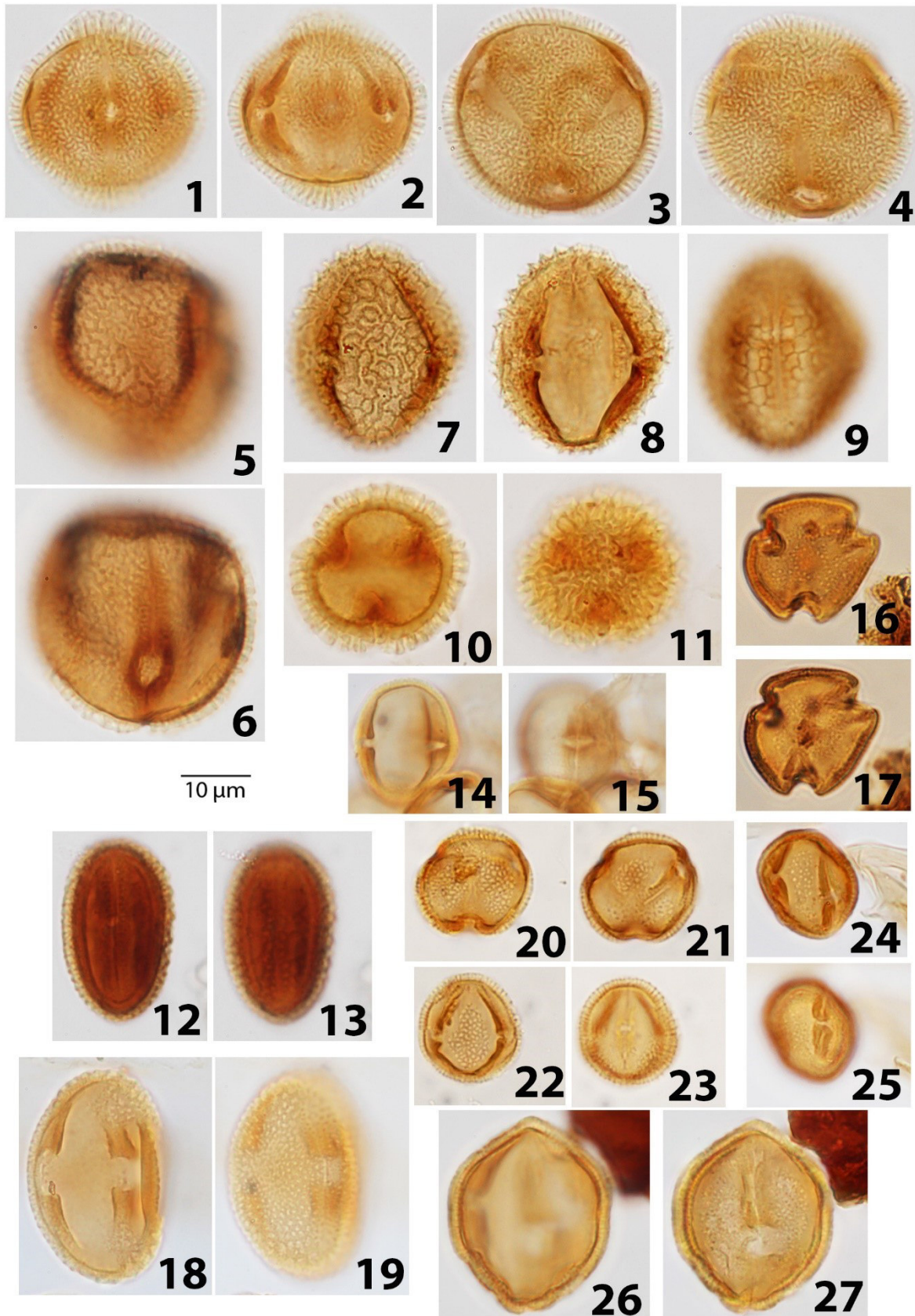


Plate 18

- 1-3. *Rhoipites crassnexinicus* sp. nov. (Holotype)
4. *Rhoipites crassnexinicus* sp. nov. (Paratype)
- 5-6. *Rhoipites guianensis* (Van der Hammen and Wymstra 1964) Jaramillo and Dilcher 2001
- 7-8. *Rhoipites guttus* sp. nov.
- 9-10. *Retitricolporites nanus* sp. nov.
- 11-12. *Rhoipites oblatum* Hoorn 1994 nov. comb.
- 13-14. *Rhoipites poropartitus* sp. nov.
15. *Rhoipites protoguttus* sp. nov. (Holotype)
- 16-17. *Rhoipites protoguttus* sp. nov. (Paratype)
- 18-19. *Rhoipites pseudocrassopolaris* sp. nov.
- 20-21. *Rhoipites pseudopilatus* sp. nov.
- 22-23. *Rhoipites ticunaensis* sp. nov. (Holotype)
- 24-25. *Rhoipites ticunaensis* sp. nov. (Paratype)



# Plate 18

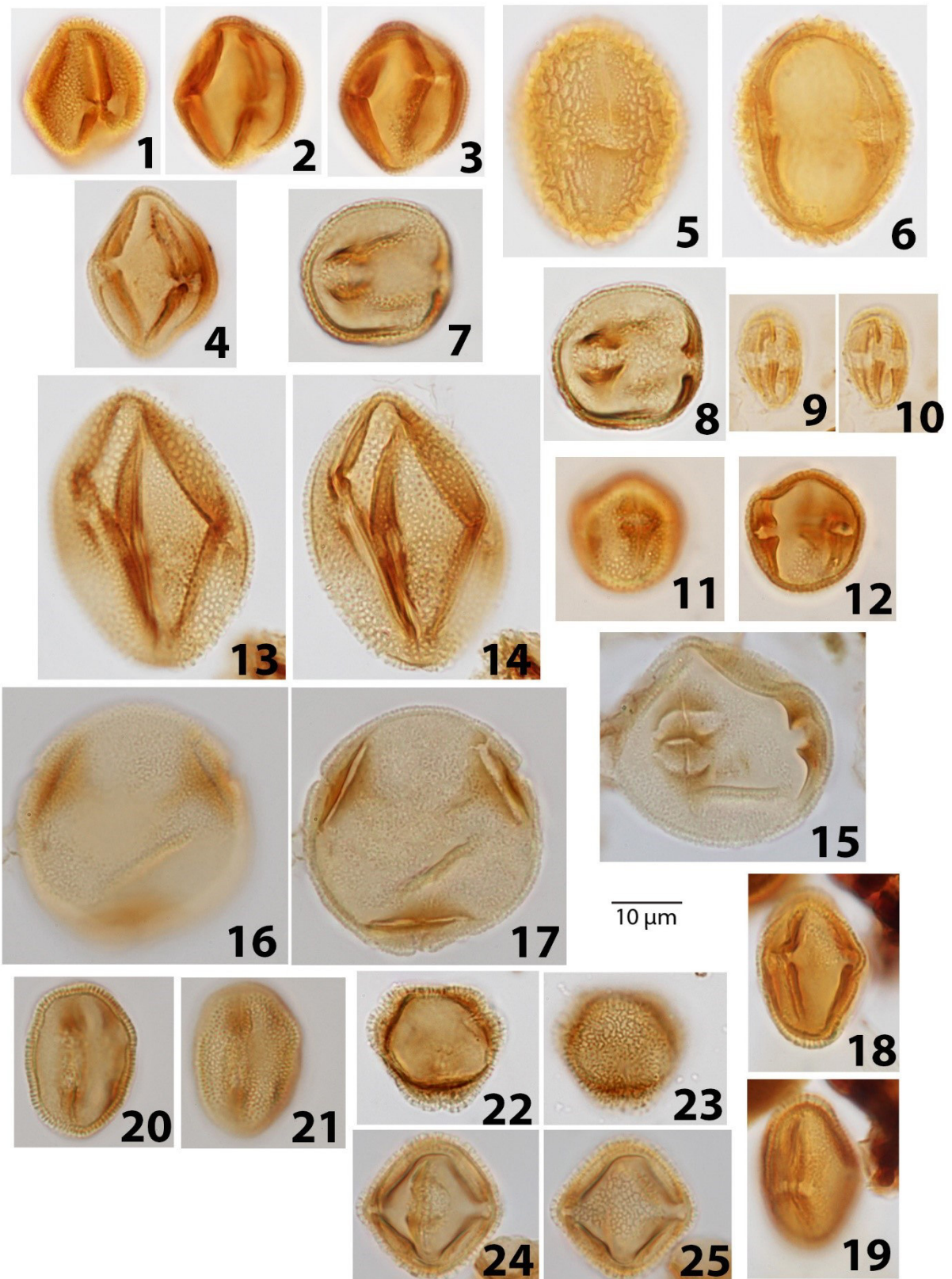


Plate 19

1-3. *Rhoipites toigoi* sp. nov. (Holotype)

4. *Rhoipites toigoi* sp. nov. (Paratype)

5-6. *Rugutricolporites arcus* Hoorn 1993

7-10. *Rugutricolporites felix* Gonzalez 1967

11-12. *Siltaria dilcheri* Silva-Caminha *et al.* 2010

13-14. *Siltaria santaisabelensis* (Hoorn 1994) Silva-Caminha *et al.* 2010

15-17. *Striasyncolpites anastomosatus* Silva-Caminha *et al.* 2010

## Plate 19

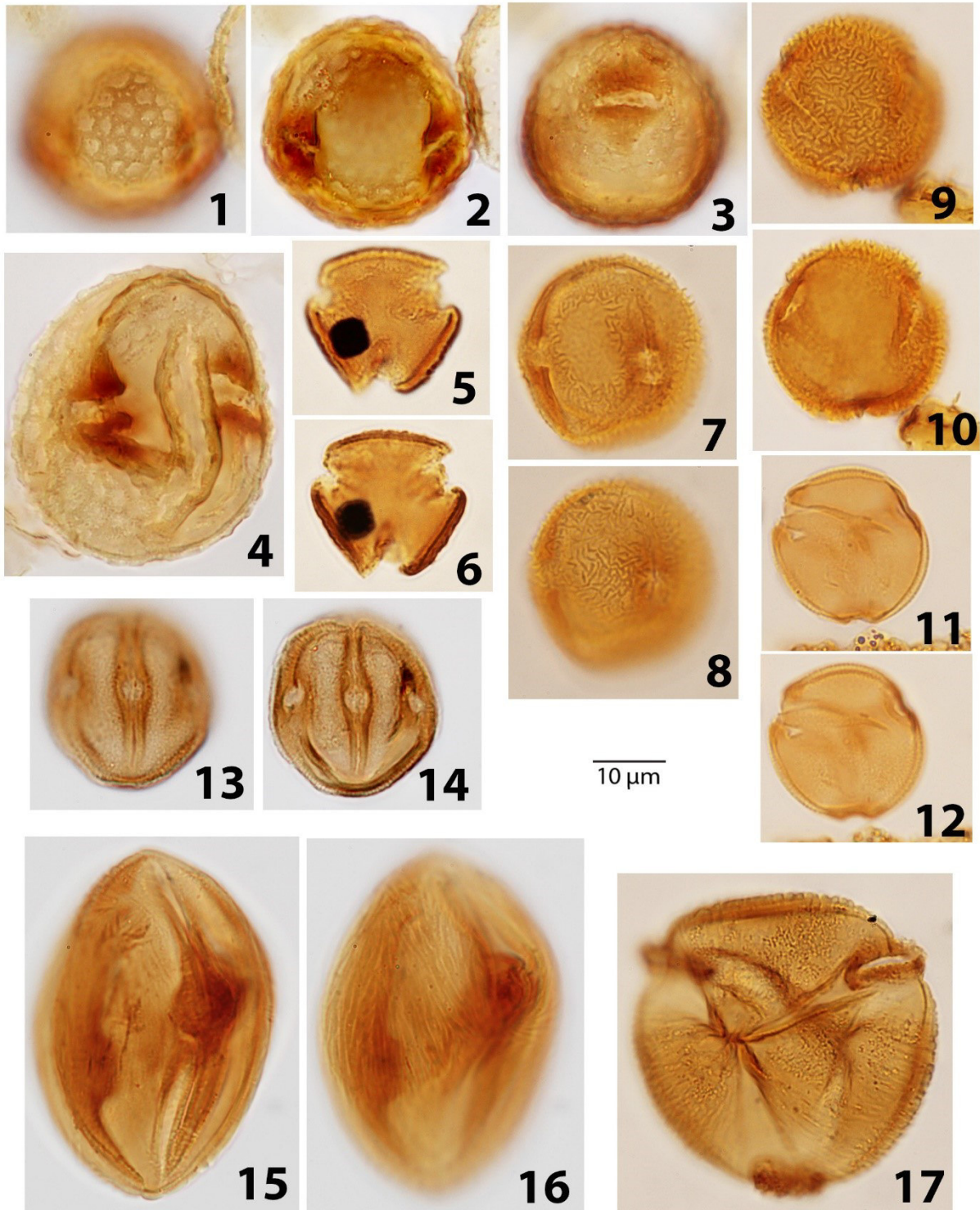


Plate 20

- 1-2. *Striatopollis catatumbus* (Gonzalez 1967) Takahashi and Jux 1989
- 3-4. *Striatopollis macrolobium* sp. nov. (Holotype)
5. *Striatopollis macrolobium* sp. nov. (Paratype)
- 6-7. *Striatopollis poloreticulatus* Silva-Caminha *et al.* 2010
- 8-9. *Syncolporites triangularis* Regali *et al.* 1974
- 10-11. *Verrutricolporites pequenus* sp. nov.
- 12-13. *Verrutricolporites rotundiporus* Van der Hammen and Wymstra 1964
- 14-15. *Verrutricolporites simplex* (Holotype)
- 16-17. *Verrutricolporites simplex* (Paratype)
- 18-19. *Zonocostites ramonae* Germeraad *et al.* 1968
- 20-21. *Byttneripollis ruedae* Silva-Caminha *et al.* 2010
- 22-23. *Byttneripollis rugulata* nov. sp. (Holotype)
- 24-25. *Byttneripollis rugulata* nov. sp. (Paratype)



## Plate 20

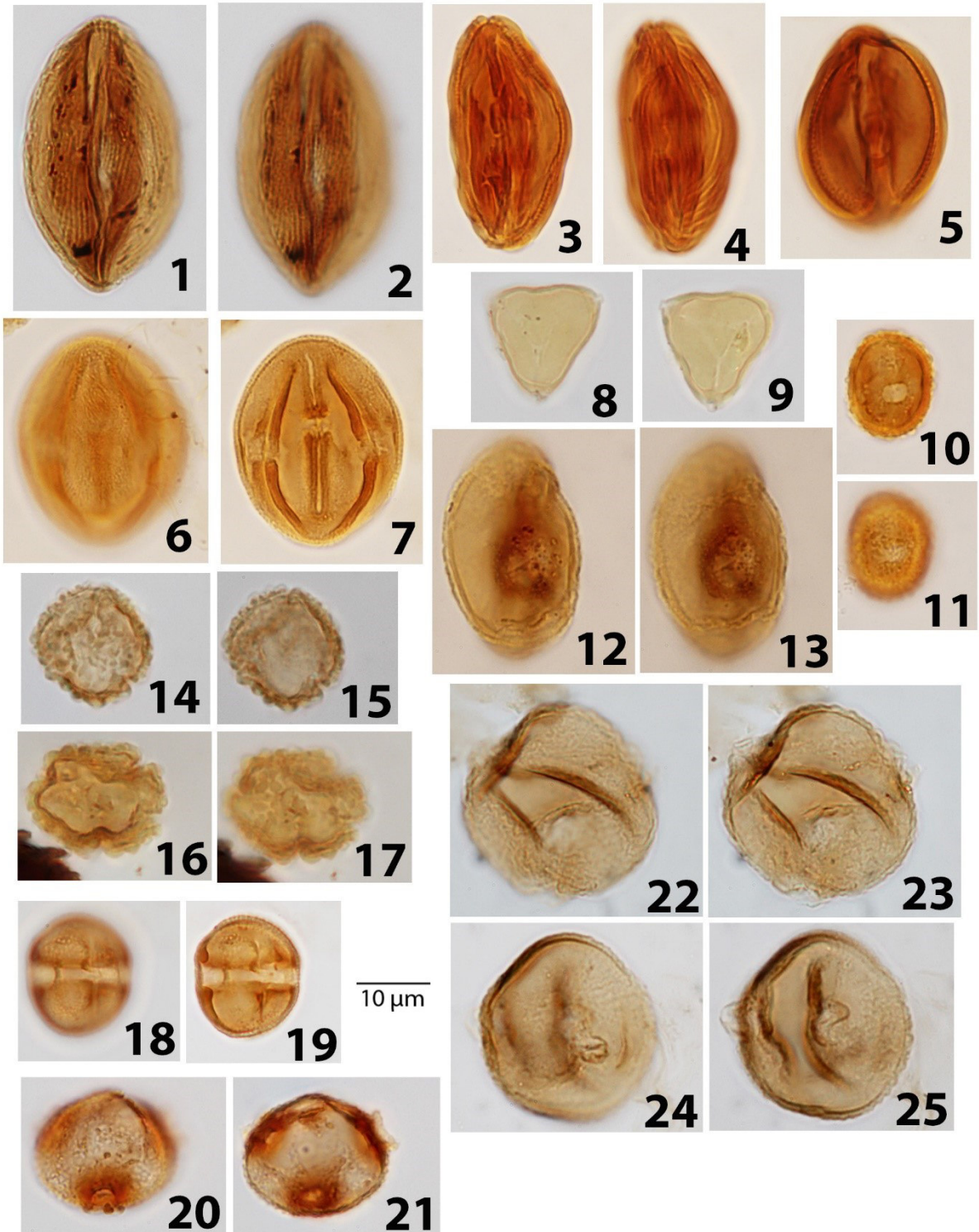


Plate 21

1. *Corsinipollenites collaris* Silva-Caminha *et al.* 2010
- 2-3. *Corsinipollenites oculusnoctis* (Thiergart 1940) Nakoman 1965
4. *Corsinipollenites scabratus* Silva-Caminha *et al.* 2010
- 5-6. *Foveotriporites? nodus* sp. nov.
- 7-8. *Proteacidites poriscabratus* sp. nov. (Holotype)
9. *Proteacidites poriscabratus* sp. nov. (Paratype)
10. *Proteacidites pseudodehaani* sp. nov.
11. *Proteacidites triangulates* Lorente 1986
12. *Psilatriporites desilvae* Hoorn 1993
13. *Psilatriporites minimum* sp. nov. (Holotype)
- 14-15. *Psilatriporites minimum* sp. nov. (Paratype)
- 16-17. *Psilatriporites salafrarius* sp. nov. (Holotype)
18. *Psilatriporites salafrarius* sp. nov. (Paratype)
- 19-20. *Retitriporites discretus* sp. nov. (Holotype)
- 21-22. *Retitriporites discretus* sp. nov. (Paratype)



## Plate 21



Plate 22

1-2. *Retitriporites tuberosum* sp. nov.

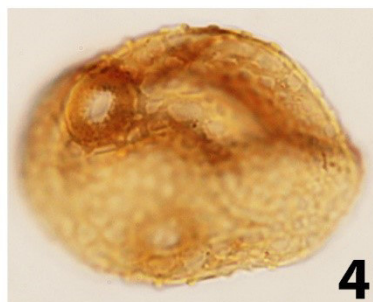
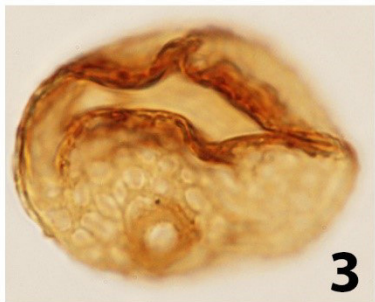
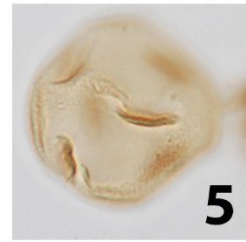
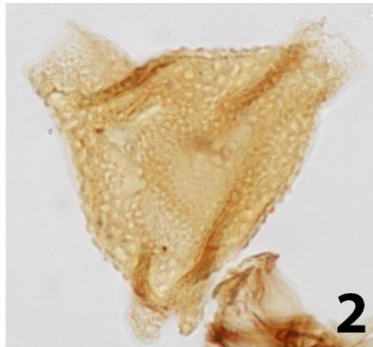
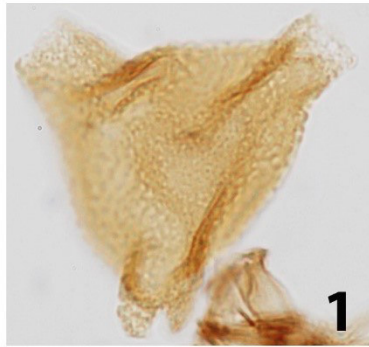
3-4. *Retitriporites typicus* Gonzalez 1967

5-6. *Lymingtonia amazonica* sp nov.

7-8. *Lymingtonia splendens* sp nov.

9-11. *Ctenolophinidites suigeneris* Silva-Caminha *et al.* 2010

## Plate 22



10  $\mu$ m

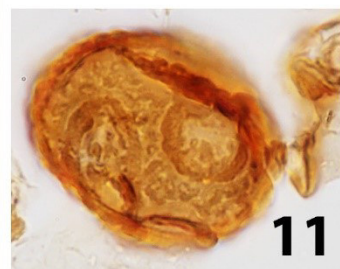
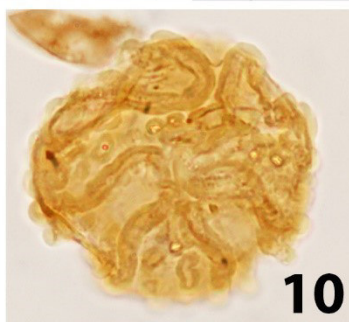
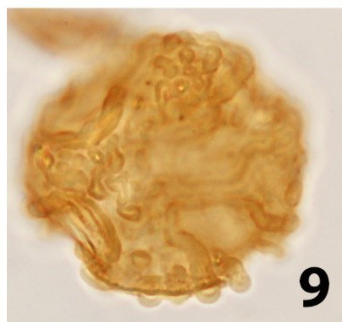
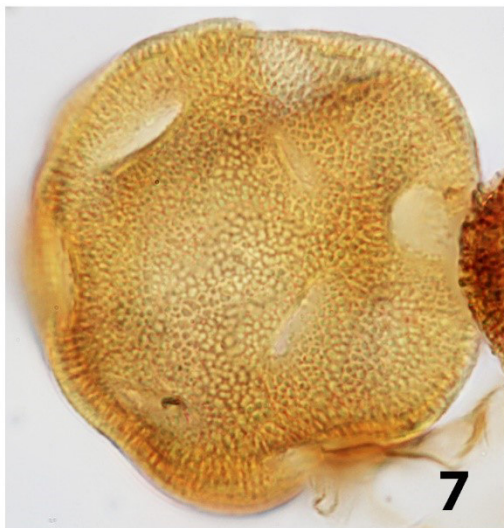


Plate 23

- 1-2. *Retistephanocolpites curvimuratus* sp. nov. (Holotype)
3. *Retistephanocolpites curvimuratus* sp. nov. (Paratype)
- 4-5. *Retistephanocolpites liberalis* sp. nov. (Holotype)
6. *Retistephanocolpites liberalis* sp. nov. (Paratype)
- 7-8. *Retistephanocolpites passionis* sp. nov. (Holotype)
9. *Retistephanocolpites passionis* sp. nov. (Paratype)
- 10-11. *Heterocolpites incomptus* Hoorn 1993
12. *Heterocolpites rotundus* Hoorn 1993
- 13-14. *Heterocolpites verrucosus* Hoorn 1993
- 15-16. *Heterocolpites brevicolpatus* Silva-Caminha *et al.* 2010
17. *Jandufouria minor* Jaramillo and Dilcher 2001
- 18-19\*. *Jandufouria seamrogiformis* Jaramillo and Dilcher 2001

\*picture is half sized



## Plate 23

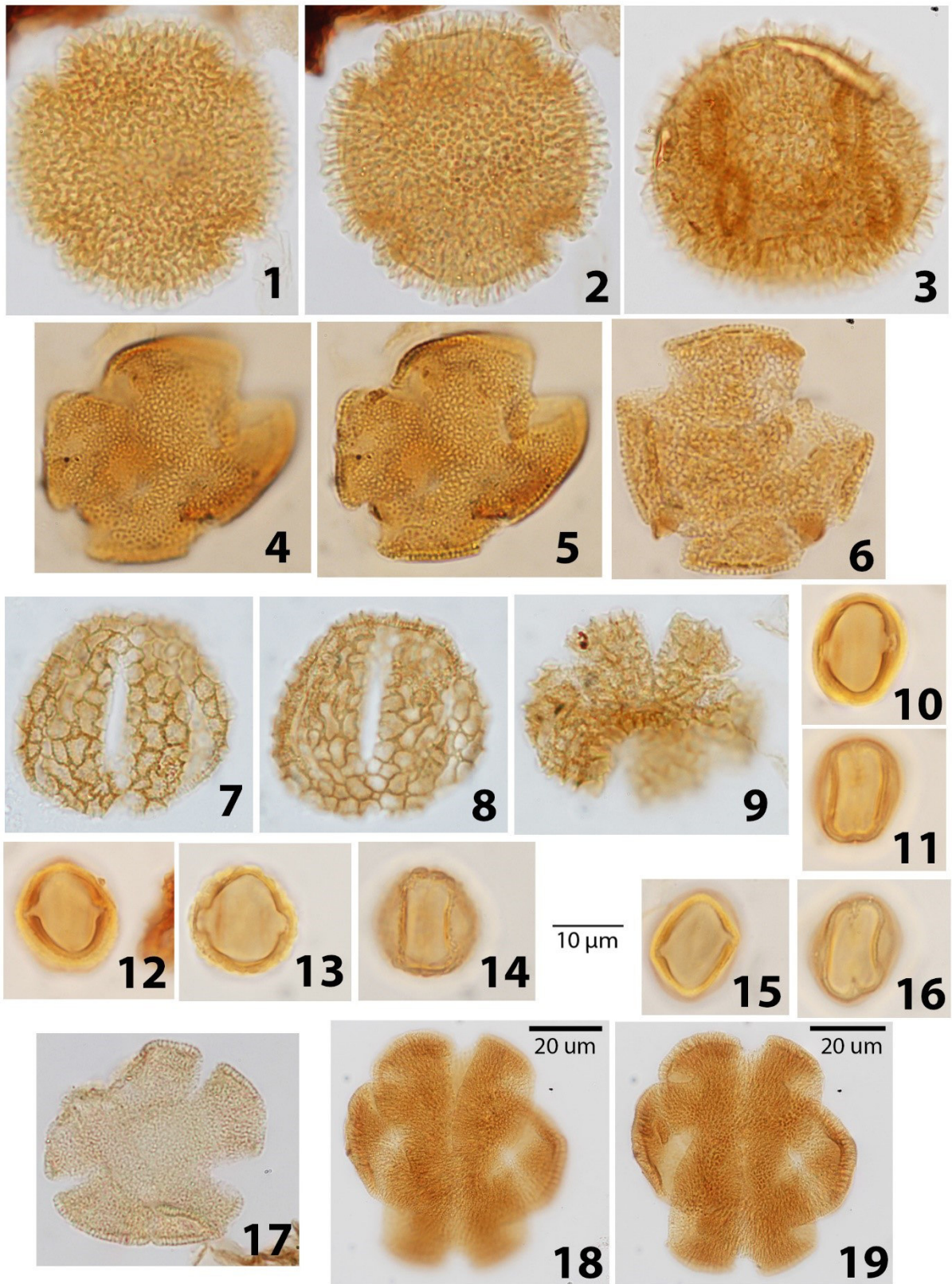


Plate 24

- 1-3. *Loxocolporites foveolatus* gen. et sp. nov.
4. *Psilastephanocolporites fissilis* Leideimeyer 1966
- 5-6. *Psilastephanocolporites marinamensis* Hoorn 1994
- 7-8. *Psilastephanocolporites meliosus* sp. nov. (Holotype)
9. *Psilastephanocolporites meliosus* sp. nov. (Paratype)
- 10-11. *Psilastephanocolporites pseudomarinamensis* sp. nov.
- 12-13. *Crotoperiporites pulcher* gen. et sp. nov.
- 14-16. *Cyperaceaepollenites cf neogenicus* Krutzsch 1970
- 17-18. *Echiperiporites akanthos* Van der Hammen and Wymstra 1964
- 19\*. *Echiperiporites estelae* Germeraad *et al.* 1968
20. *Echiperiporites intectatus* Silva-Caminha *et al.* 2010
21. *Echiperiporites jutaiensis* Silva-Caminha *et al.* 2010
- 22-23\*. *Echiperiporites lophatus* Silva-Caminha *et al.* 2010

\*picture is half sized



## Plate 24

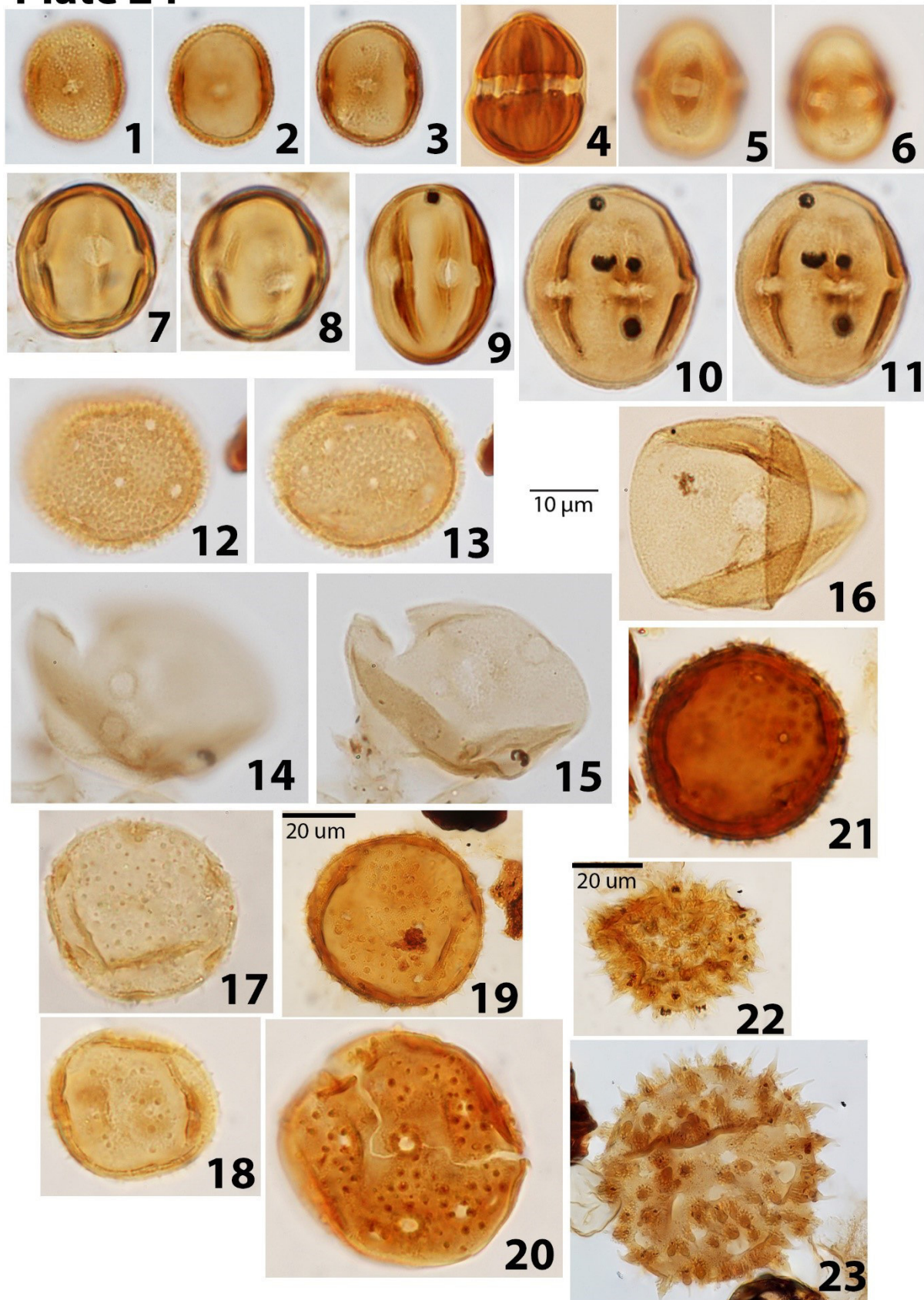


Plate 25

1. *Multiporopollenites crassinexinatus* Silva-Caminha *et al.* 2010
- 2-3. *Multiporopollenites intermedius* sp. nov.
4. *Parsonsidites? brenacii* Silva-Caminha *et al.* 2010
5. *Parsonsidites? minibrenacii* sp. nov. (Holotype)
6. *Parsonsidites? minibrenacii* sp. nov. (Paratype)
- 7-8. *Perisyncolporites grossus* nov. sp. (Holotype)
- 9-10. *Perisyncolporites pokornyi* Germeraad *et al.* 1968
11. *Psilaperiporites multiporatus* Hoorn 1994
- 12-13. *Psilaperiporites pauciporatus* nov. sp.
- 14-15. *Psilaperiporites redondus* nov. sp.
16. *Psilastephanoporites herngreenii* Hoorn 1993
17. *Retistephanoporites crassiannulatus* Lorente 1986
- 18-19. *Verrustephanoporites dubius* sp. nov.
- 20-21. *Verrustephanoporites intraverrucosus* nov. sp.



# Plate 25

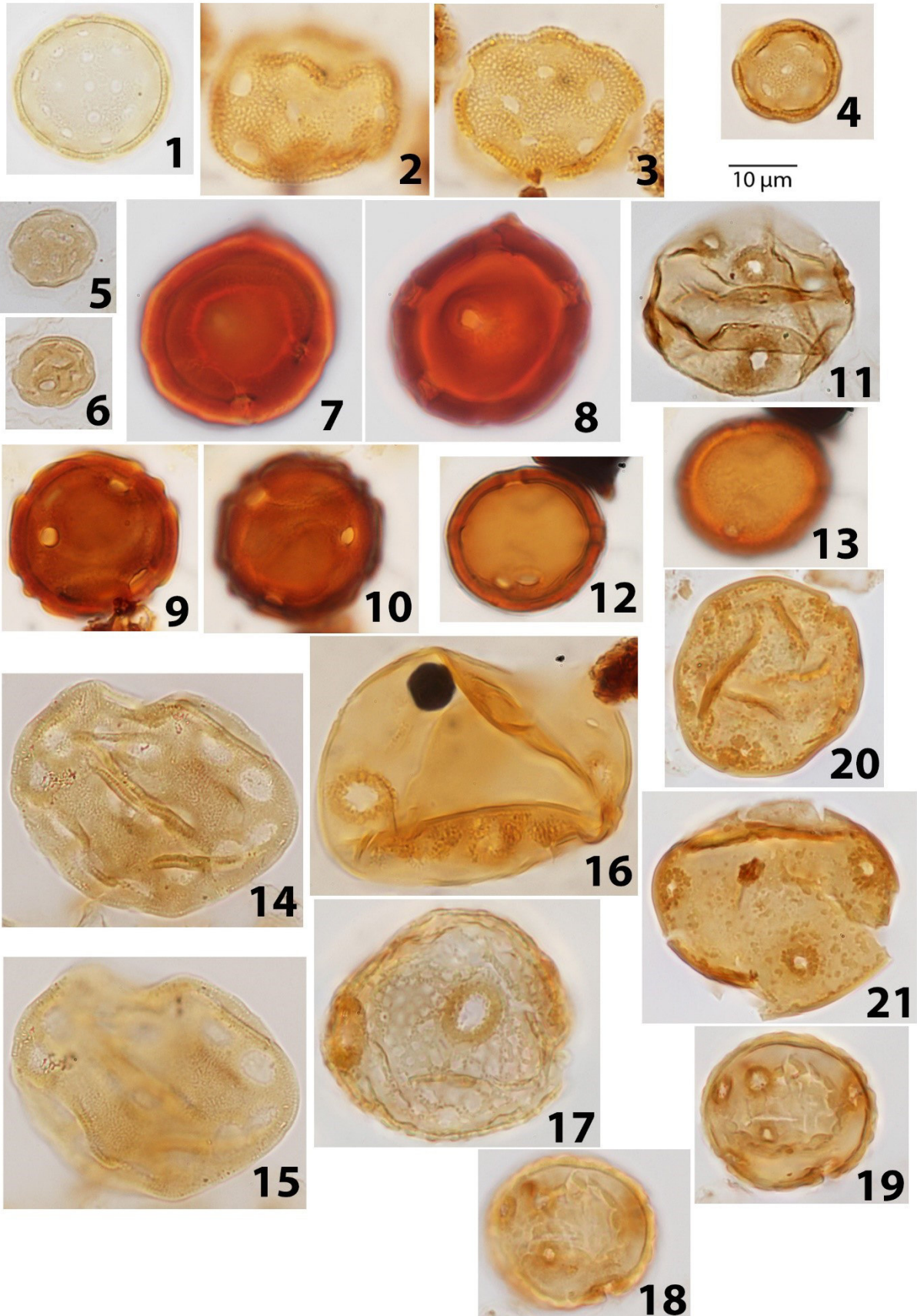


Plate 26

1. *Botryococcus* spp.
2. *Pediastrum* spp.
- 3\*. Foraminiferal lining
4. *Apteodinium?* *vescum* Matsuoka 1983
5. Rounded Brown Cysts (RBCs)
- 6-7. *Cleistosphaeridium ancyreum* (Cookson and Eisenack) Eaton *et al.* 2001
- 8-9. *Cleistosphaeridium placacanthum* (Deflandre and Cookson) Eaton *et al.* 2001
10. *Cribroperidinium* spp.
11. *Cyclopsiella elliptica/granosa* complex sensu de Verteuil and Norris 1996
- 12-13. *Hystriochokolpoma rigaudiae* Deflandre and Cookson 1955
- 14-15. *Hystriochokolpoma* spp.
- 16-17. *Impletosphaeridium prolatum* Head *et al.* 1989
- 18\*. *Leiosphaeridia* "scabrate"
- 19\*\*. *Leiosphaeridia* spp.
- 20-22. *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall 1967

\*picture is doubled-sized

\*\*pictures 18 and 19 were taken with phase contrast

# Plate 26

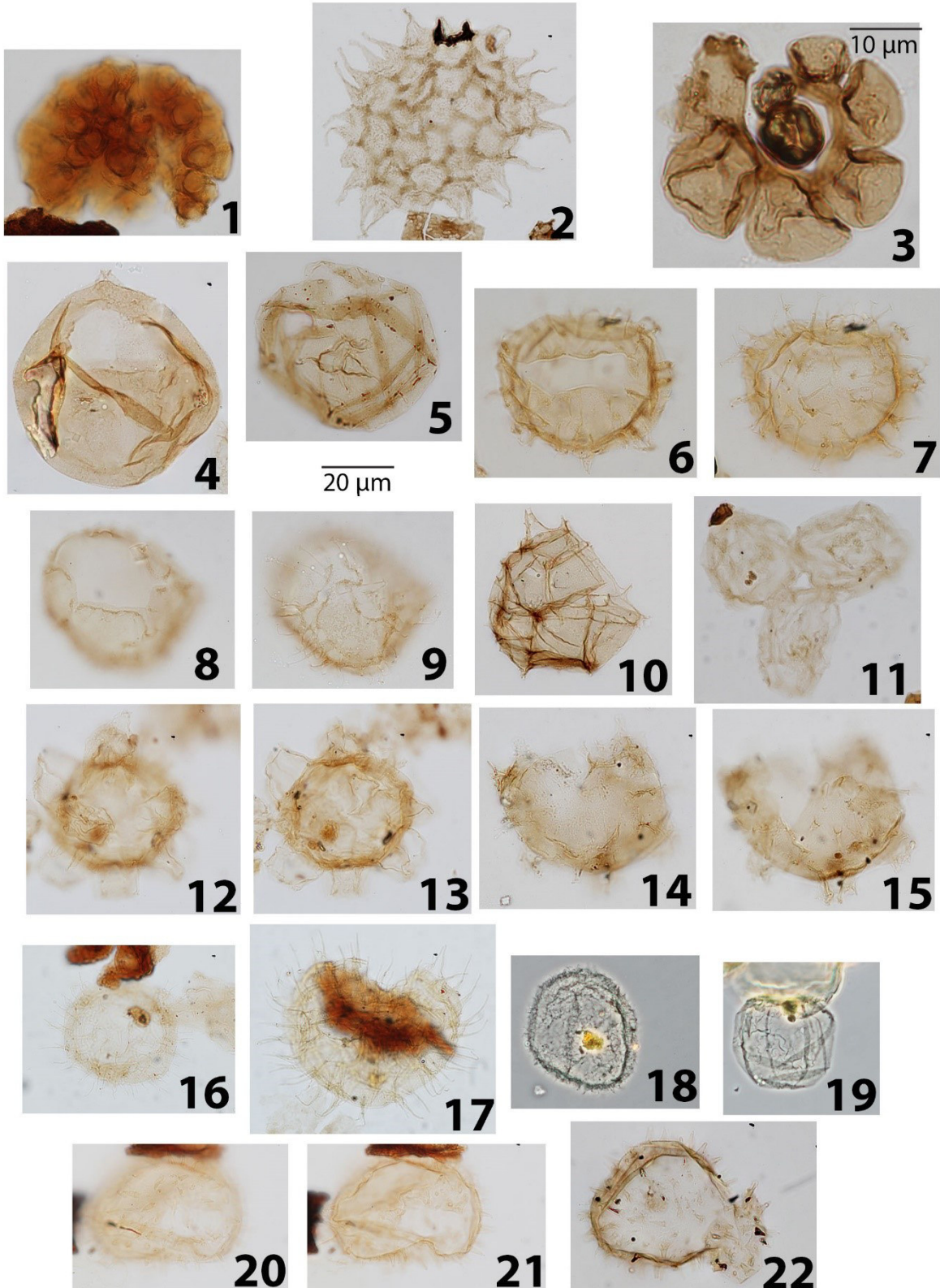
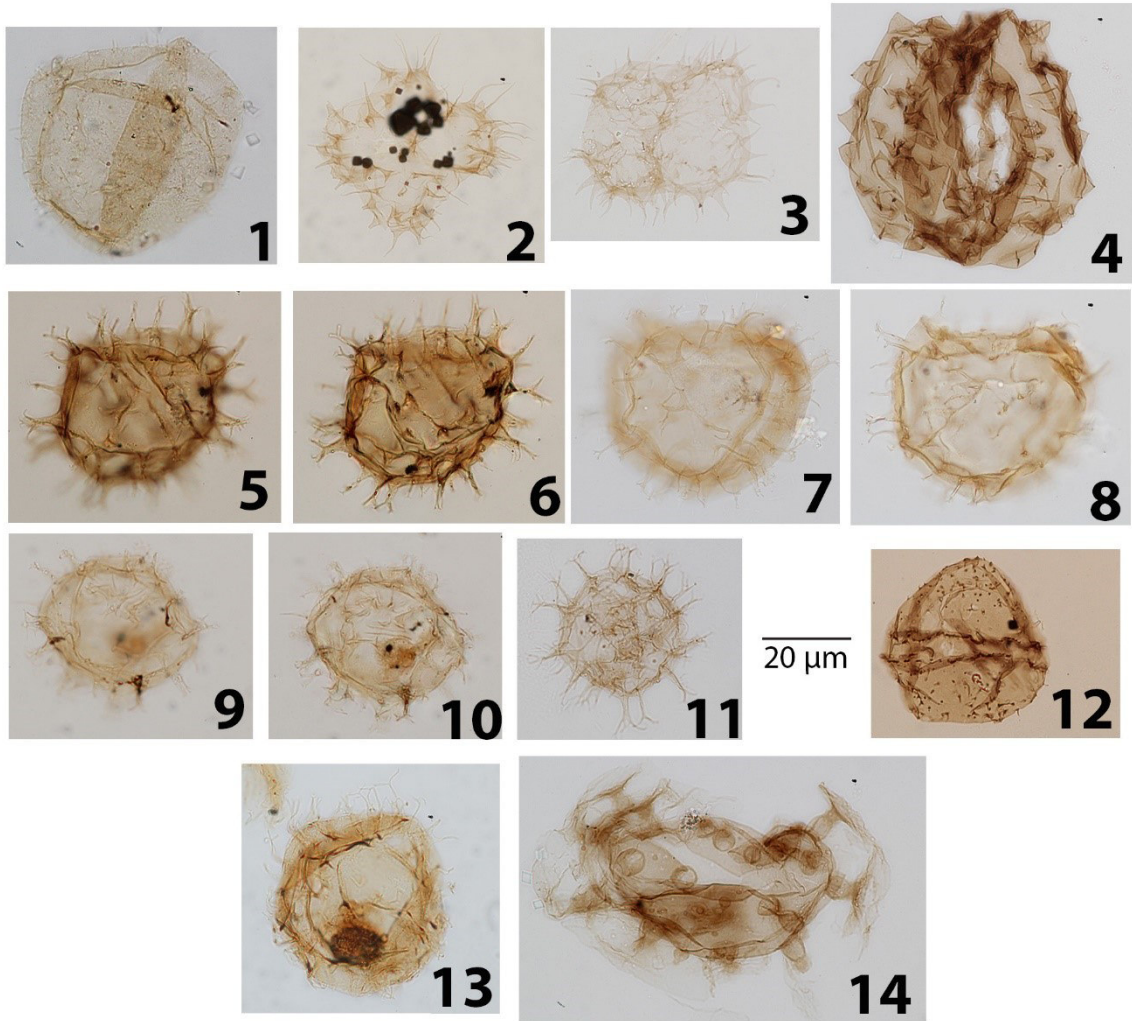




Plate 27

1. *Operculodinium israelianum* (Rossignol) Wall 1967
- 2-3. *Quadrina? condita* de Verteuil and Norris 1996
4. *Quadrina? "incerta"* (= Dinocyst XI of Lenoir and Hart, 1986)
- 5-8. *Spiniferites "normalis"*
- 9-11. *Spiniferites* spp.
12. *Trinovantedinium ferugnomatum* de Verteuil and Norris 1996
13. *Trinovantedinium? Xylochoporum* de Verteuil and Norris 1996
14. *Tuberculodinium vancampoe* (Rossignol) Wall 1967

## Plate 27



## Chapter 5: Biostratigraphy

### 5.1. Introduction

Dating core 1-AS-105-AM was not only an objective of the current work but also a step without which the subsequent thesis aims could not be reached. In order to build an age model for the core, palynology was used as the main source of information. This was due to pollen data being abundant throughout the complete core and because the most updated biozonation in northwestern South America is based on pollen (Jaramillo *et al.* 2011). Other source of information was dinoflagellates and molluscs, however both of them are heavily controlled by facies and restricted to few samples, so they served only as complementary means of dating. Nevertheless, when these different organism groups agree in their age indications, even if roughly, it gives confidence to the biostratigraphy applied. Pollen data was subject to Graphic Correlation (see methods in Chapter 3), whose results propose an age model against which other sections in the Solimões Formation are compared to.

### 5.2. Palynostratigraphical framework

The biostratigraphical framework used in western Amazonia has been largely based on work carried out in Venezuela and Colombia. In Venezuela, pollen work was developed by Germeraad *et al.* (1968), Lorente (1986) and Muller *et al.* (1987), their zonations were adapted by Hoorn (1993, 1994a, 1994b) for use in western Amazonia. The sequence of events from Lorente (1986) fitted well the events seen by Hoorn, showing a good correspondence in the overall palynostratigraphical framework in different parts of northwestern South America. Nevertheless, some problems arose when regional correlations were made. Inconsistencies were pointed by Latrubesse *et al.* (2007, 2010), who also used Lorente's zones to date sections in western Amazonia. Such inconsistencies were related to stratigraphic ranges of marker taxa overlapping zone boundaries. More recently, a zonation

erected by Jaramillo *et al* (2011) and with much better age calibrations showed that some important taxa have older first appearances than what previously postulated, despite also showing good correspondence with the Venezuelan zonations (Germeraad *et al.* 1968, Muller *et al.* 1987). An example is *Grimsdalea magnaclavata*, probably the most used marker taxa in north-western South America. These issues are especially critical when entire sections are placed within one single pollen zone, which is the case with many small outcrops. For instance, zone Grimsdalea (Fig. 5.1) ranges from 16 to 14 Ma, but the taxon *G. magnaclavata*'s range extends from latest early Miocene to the mid-late Pliocene – a significantly longer time interval.

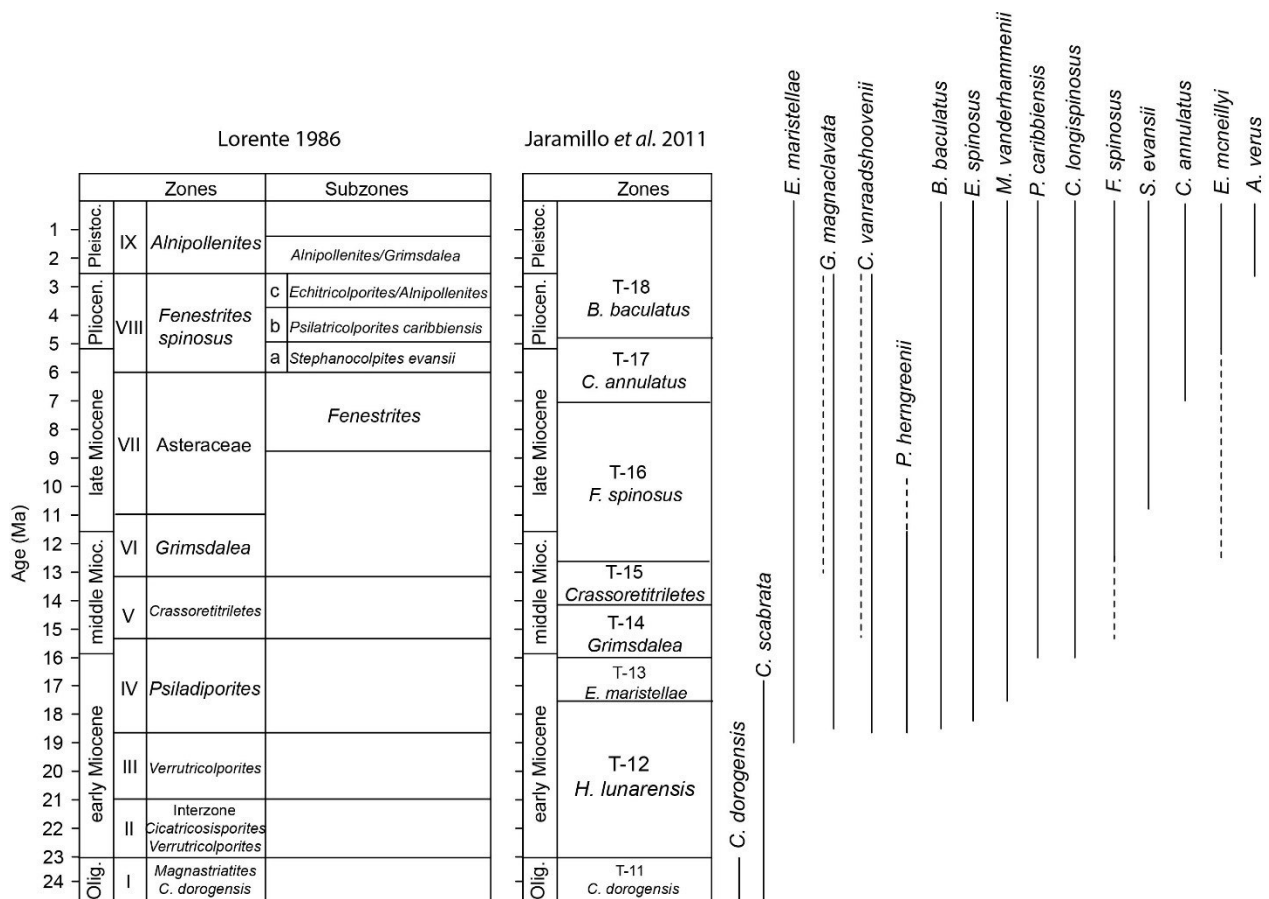


Fig. 5.1. The two principal palynological zonations used in Amazonia, from Venezuela (Lorente 1986) and from the Llanos and Llanos foothills of Colombia (Jaramillo *et al.* 2011). Taxa ranges (on the right) were adapted from Jaramillo *et al.* (2011) with modifications from Jaramillo *et al.* (in prep), some differences are evident. Dashed lines are uncertainties in ranges. *Grimsdalea magnaclavata* and *Crassoretitriletes vanraadshoovenii* have two ranges shown (dashed line: Lorente 1986; solid line: Jaramillo *et al.* 2011). *Echitricolporites maristellae* = *Malvacipolloides maristellae* (Silva-Caminha *et al.* 2010); *Psilatricolporites caribbiensis* = *Ladakhpollenites caribbiensis* (Silva-Caminha *et al.* 2010).

As new sites are discovered and analysed, zonations are updated, and the continuous reassessment of ages is necessary. Here, I take advantage of recent developments and inclusion of new sites in the zonation of Jaramillo *et al.* (2011) to date core 105-AM studied herein and correlate it with sites in western Amazonia and from the work of previous authors.

### **5.3. Graphic Correlation (age model)**

Graphic correlation was performed between core 105-AM (this thesis) and the composite section of Jaramillo *et al.* (2011). In its recent update (Jaramillo *et al.* in prep) the composite section included sites in western Amazonia. Of special interest among these sites is Saltarin in the Colombian llanos (Fig. 1.2). Saltarin is a ~700 metres deep cored section ranging from Early Miocene to the Pliocene, it has excellent pollen recovery almost throughout the entire core and marine incursions were detected. Additional events other than first and last appearances of species were also used. These were surfaces of marine incursions, which make excellent correlation points, as well as sequence stratigraphy points (Appendix 9.4). It is important to note that the base of the age model is the Graphic Correlation performed using palynomorphs, and that sequence stratigraphy points were only added to refine the line of correlation, but without major changes. The lower and upper limits of marine incursions were delimited according to the peak abundance of marine elements (i.e. an ACME event). This was done to ensure the peak of the event is isolated from its full stratigraphic cover that can vary among different geographical areas whereas the peak abundance will tend to be more homogeneous over broad areas. The full list of events used for all rounds of correlations can be found in Appendix Tables 9.1.a) to 9.1.d). Codes for producing Line of Correlations (LOC) can be found in the Appendix (9.1.e) and f)). Range-charts with all species counted in the core can be found in Appendix 9.1.g).



*Correlation 1-AS-105-AM vs. composite section (Fig. 5.3 Table 5.1):*

At the bottom of section 105-AM three FADs of important taxa are in full agreement with the FAD events in the composite section. These taxa are *Ilexpollenites tropicalis*, *Grimsdalea magnaclavata* and *Bombacacidites baculatus*. This established the initial correlation point. Following it, the lower marine incursion and its associated FADs of dinocysts constituted another important step in the line of correlation. Towards the middle and upper parts of the 105-AM section, the key marker taxa *Cichoreacidites longispinosus*, *Retitricolporites crassicostatus* and *Fenestrites spinosus* have their FADs and *Psilastephanoporites herngreenii* and *Echidiporites barbeitoensis* have their LADs. These events constrained the terminal part of the line of correlation. Some useful sequence stratigraphy events were C2-I2, C2-I3H, C1-I1, C1-12, L-12, L-13 and L-15 (their description can be found in the Appendix material), they mostly represent maximum flooding surfaces within parasequences. They were added to the composite section after being also identified in core Saltarin (Fig. 5.3).

After the line of correlation was established, depths in core 105-AM were transformed into composite units. These units have ages associated to them from a calibration of the composite section by means of foraminiferal biostratigraphy, magnetostratigraphy and carbon isotopes (Fig. 5.4; and Jaramillo *et al.* 2011). Therefore, ages for all composite units in core 105-AM could be generated. Samples between each pair of composite units were interpolated linearly. Likewise, samples after the topmost and before the bottommost samples were extrapolated linearly. The final result is an age-depth curve ranging from 18.78 to 10.72 Ma (Fig. 5.4). Sample interval gap has an average time span of 0.08 Ma (min. 0.01 and max. 0.32). These ages are a working model, naturally prone to changes as new calibration points are added to the composite section. Their use is not intended with the same precision as in absolute dating methods, but they provide an age framework so far not tried in western

Amazonia and therefore formulate a baseline on which biostratigraphical hypotheses can be built on for future improvements.

Table 5.1. Key biostratigraphic markers used for graphic correlation (Fig. 5.2). Range charts with the distribution of all species identified can be found in Appendix 9.1.g.

Event/Taxa	Depth in 105-AM	Depth in S.C.S.	Comments
FAD <i>G. magnaclavata</i>	-326.2	-9,777.74	This FAD is widely recognized as a marker of the middle or latest early Miocene*
FAD <i>I. tropicalis</i>	-324.9	-9,799.83	Added to the S.C.S. after correlation with Saltarin
FAD <i>B. baculatus</i>	-325.3	-9,777.74	This FAD is widely recognized as a marker late early Miocene (ca. 17.35 Ma)
FAD FL EM	-293.3	-9,535.84	Added to the S.C.S. after correlation with Saltarin
LAD FL EM	-284	-8,511.18	Added to the S.C.S. after correlation with Saltarin
FAD <i>C. longispinosus</i>	-165.5	-5,492.8	This FAD is at app. 10 Ma in Jaramillo <i>et al.</i> (2011), but with uncertainties, now it is clearly older (ca. 16 Ma) after correlation with Saltarin
FAD <i>R. crassicosatus</i>	-125.3	-4,647.01	Added to the S.C.S. after correlation with Saltarin
FAD <i>F. spinosus</i>	-75.3	-4,039.3	FAD is a zone marker, at app. 10 Ma in Jaramillo <i>et al.</i> (2011)
LAD <i>P. herngreeni</i>	-359	-9,129.27	This LAD is at ca. 11.8 Ma in Jaramillo <i>et al.</i> (2011)
LAD <i>E. barbeitoensis</i>	-105.5	-5,194.03	Had not yet been applied in w. Amazonia, in Venezuela it is a mid. Miocene marker
FAD FL MM	-101.2	-5,342.95	Added to the S.C.S. after correlation with Saltarin
LAD FL MM	-96.7	-3,959.46	Added to the S.C.S. after correlation with Saltarin

FAD = First appearance datum; LAD = Last appearance datum; FL = Flooding; EM = early Miocene; MM = middle Miocene. \*FAD age is ca. 18 Ma and ca. 16 Ma for consistent FAD.

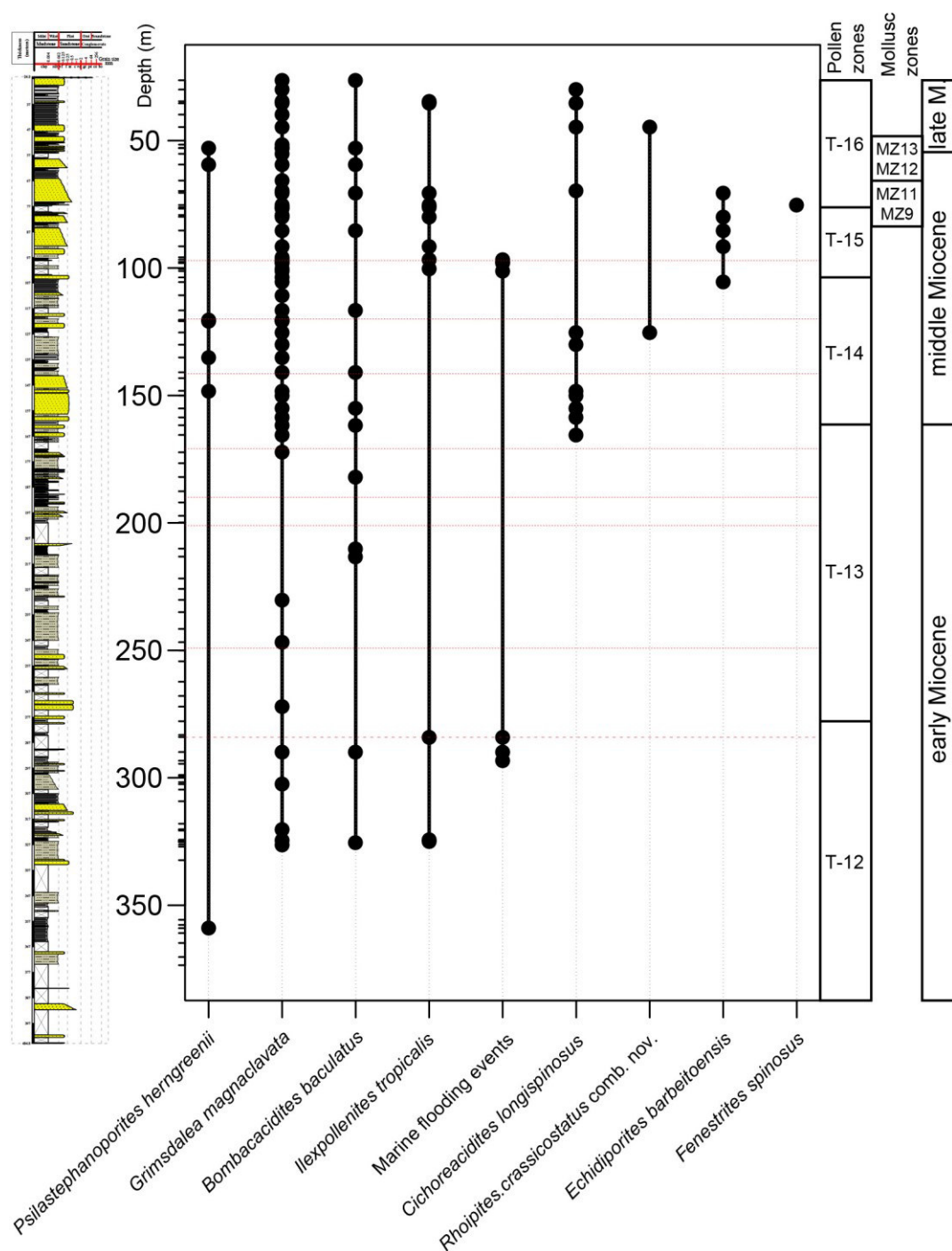


Fig. 5.2. Range chart of selected palynomorphs used for graphic correlation. Pollen zones follow Jaramillo *et al.* (2011), for more details see Fig. 5.1 and Table 5.1. Mollusc zones follow Wesselingh *et al.* 2006a, for more details see Fig. 5.6 and Table 5.2 and text below (5.4).

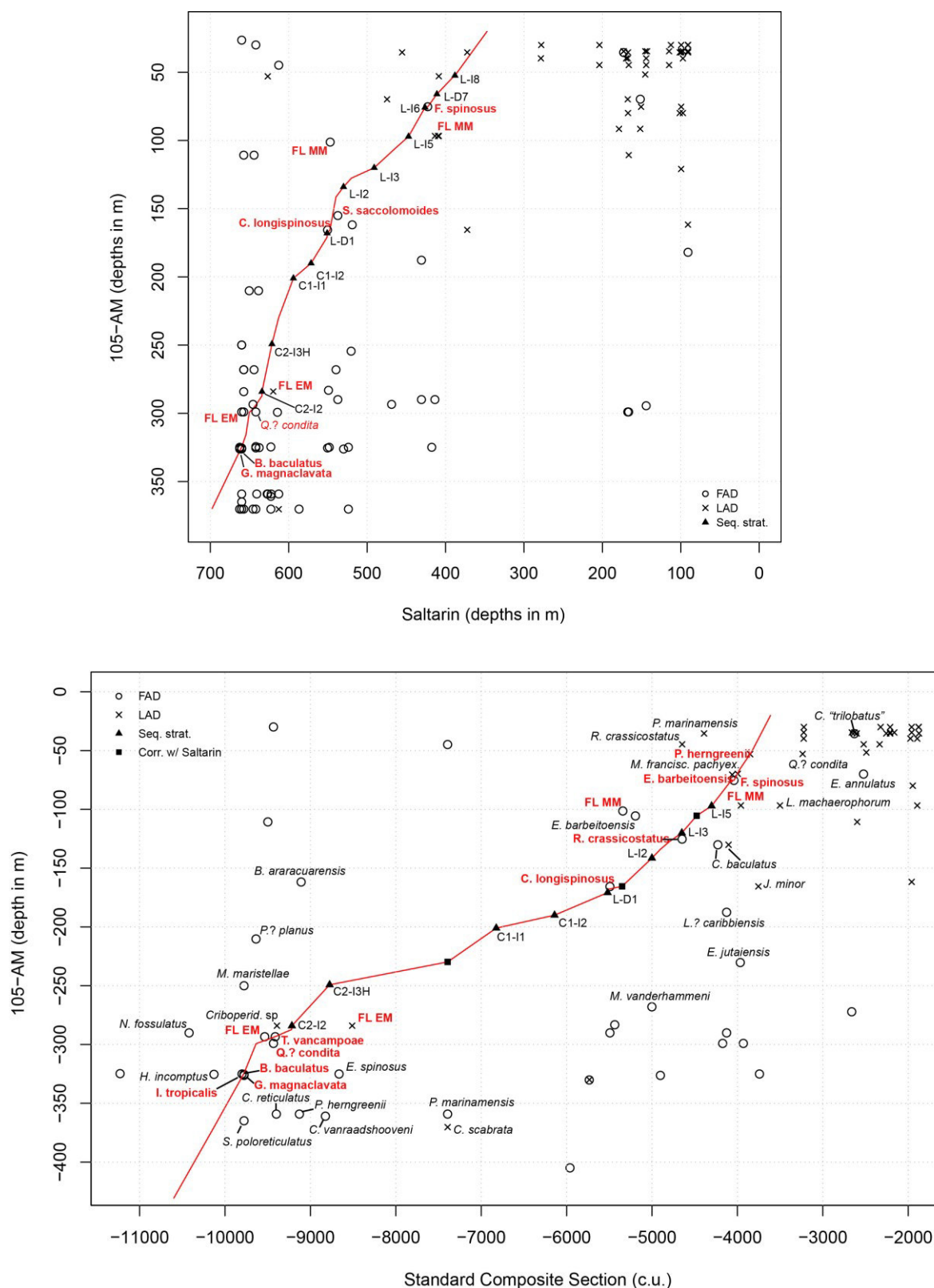


Fig. 5.3. Top: Graphic correlation between cores 105-AM and Saltarin; Bottom: graphic correlation between core 105-AM and the composite section of Jaramillo *et al.* (2011). In this plot, events of the composite section are the final round of correlation not including core 105-AM. The latest sequence of events includes core 105-AM (e.g. taxa range in Figure 5.1).

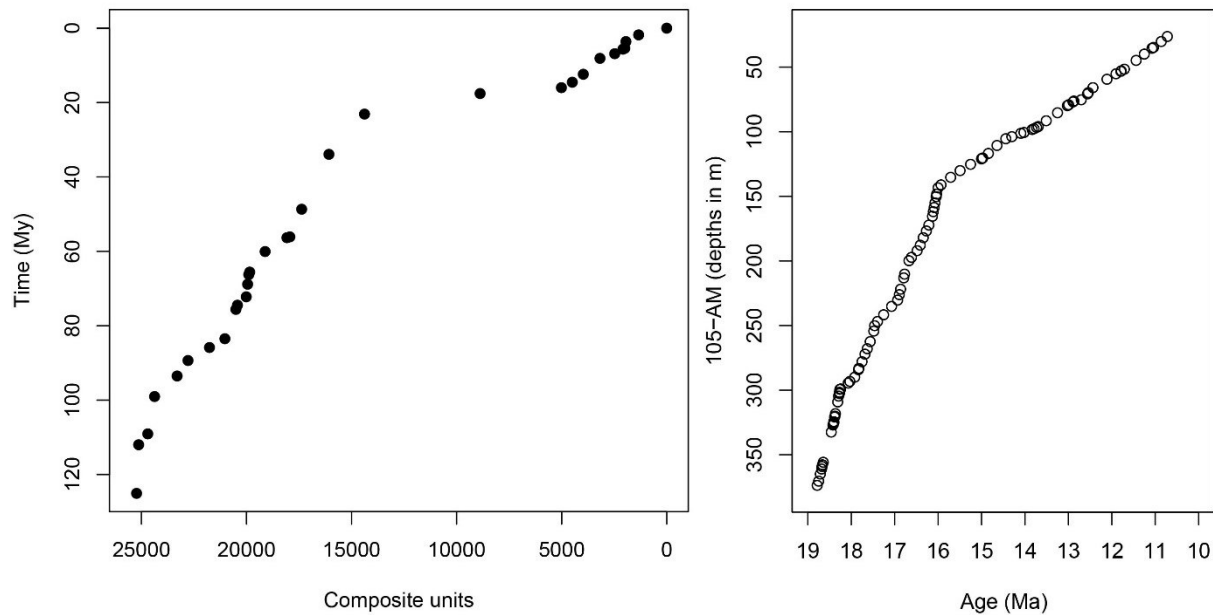


Fig. 5.4. Left: calibration of the pollen zonation of Jaramillo *et al.* (2011). Right: Age vs. Depth model for core 105-AM.

#### 5.4. Molluscs biostratigraphy

Molluscs in core 105-AM were found in four different depths and can be divided into two assemblages: 52.9 to 53 m, and 79.9 to 83 m. Twenty one species in 11 genera were identified (Table 5.2) and photographed (Fig. 5.5). The molluscan biostratigraphic zones follow Wesselingh *et al.* (2006a, 2006b), who erected a molluscan zonation for the Neogene of western Amazonia. The 52.9-53m assemblage could be assigned to either MZ12 zone (the youngest published Pebas fauna so far) but has even more in common with the yet unpublished MZ13 fauna (F. Wesselingh *personal communication*). Age would be latest middle Miocene or earliest late Miocene. The 79.9-83m assemblage seems to contain an admixture of several faunas. *Charadreon intermedius* is known from MZ7-MZ8, but most of the fauna is typical of MZ9-11 (e.g. *Aylacostoma browni*, *Charadreon glabrum*, *Pachydon trigonalis*). Therefore, the assemblage is assigned to zones MZ9-MZ11 (Late Middle Miocene). The age of both assemblages supports the age derived from graphic correlation (Fig 5.6).

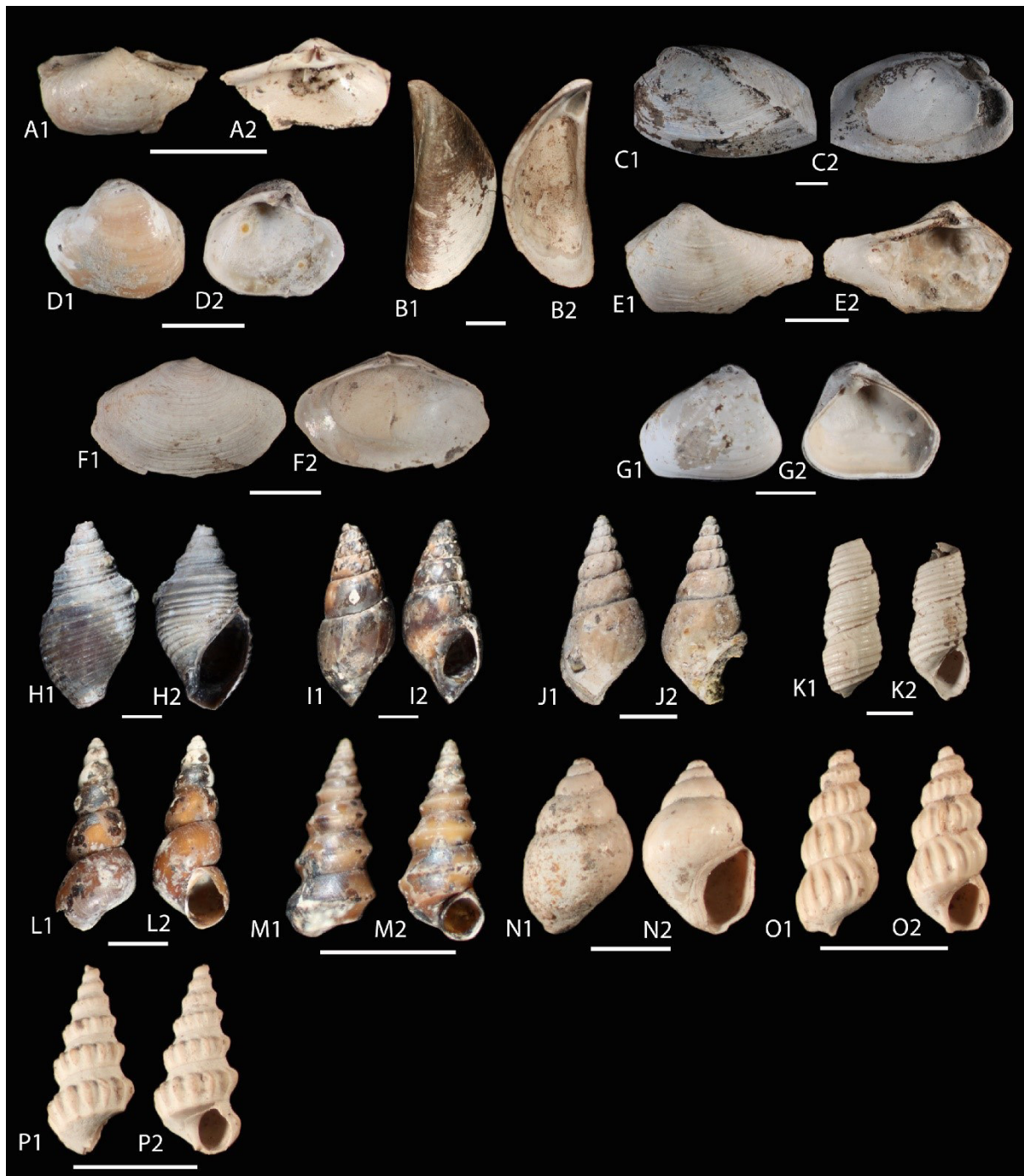


Figure 5.5. Photographs of shells from core 1-AS-105-AM. Scale bar is 2.5 mm. (A) to (G) are bivalves for which exterior and interior views are shown (1's and 2's, respectively). (H) to (P) are gastropods for which rear and front views are shown (1's and 2's, respectively). (A). *Corbula cotuhensis* Wesselingh, 53 m. (B). *Mytilopsis sallei* Récluz, 53m. (C). *Pachydon carinatus* Conrad, 83m. (D). *Pachydon cuneatus* Conrad, 52.9m. (E). *Pachydon ledaeformis* Dall, 53 m. (F). *Pachydon telliniformis* Wesselingh, 53 m. (G). *Pachydon trigonalis* Nuttall, 79.9 m. (H). *Aylacostoma browni* Etheridge, 53 m. (I). *Charadreon glabrum* Wesselingh, 79.9 m. (J). *Charadreon intermedius* Wesselingh, 79.9 m. (K). *Dyris bicarinatus bicarinatus* Wesselingh, 53 m. (L). *Dyris ortonii* Gabb, 79.9 m. (M). *Feliconcha feliconcha* Wesselingh, 79.9 m. (N). *Toxosoma grande* Wesselingh, 53 m. (O). *Tryonia nuttalli* Wesselingh, 53 m. (P). *Tryonia scalarioides scalarioides* Etheridge, 53 m. Identifications by F. Wesselingh.

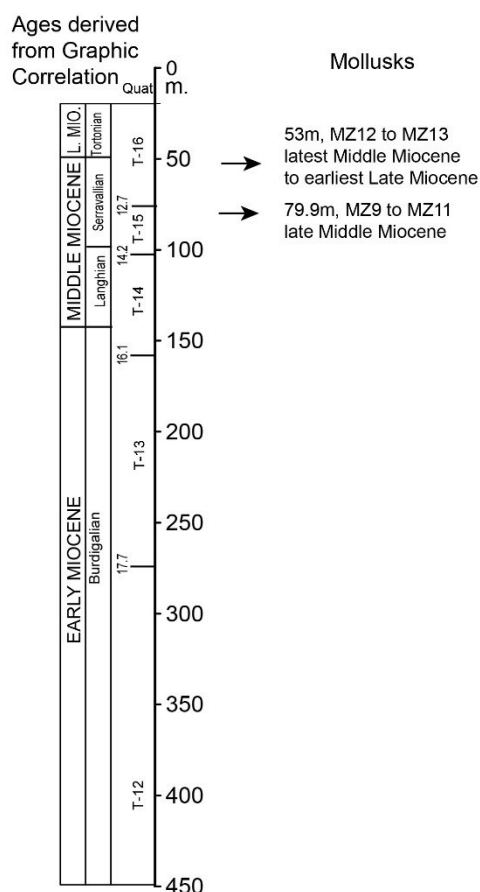


Figure 5.6. Molluscan biostratigraphy of core 105-AM. Molluscs at meter 53 indicate zone MZ12 to MZ13 (latest middle Miocene to earliest late Miocene). Assemblage at meter 79.9m indicates zone MZ9 to MZ11 (molluscan Zones after Wesselingh *et al.* 2006a). Molluscan biostratigraphy supports the ages derived from Graphic Correlation.

Table 5.2. Molluscs in core 1-AS-105-AM.

Taxa / Depth (in metres)	Assemblage 1		Assemblage 2	
	52.9	53	79.9	83
<i>?Cochliopina bourguyi</i>		1		
<i>Aylacostoma browni</i>		1	1	
<i>Charadreon glabrum</i>			1	
<i>Charadreon intermedius</i>			1	
<i>Corbula cotuhensis</i>		1		
<i>Dyris bicarinatus bicarinatus</i>		1		
<i>Dyris ortonii</i>			1	
<i>Dyris</i> sp.		1		
<i>Feliconcha feliconcha</i>			1	
<i>Mytilopsis sallei</i>		1		
<i>Pachydon carinatus</i>				1
<i>Pachydon cuneatus</i>	1			
<i>Pachydon ledaeformis</i>		1		
<i>Pachydon telliniformis</i>		1		
<i>Pachydon trigonalis</i>			1	
<i>Sheppardiconcha cf coronata</i>	1	1		
<i>Toxosoma aff. contortum</i>		1		
<i>Toxosoma grande</i>		1		
<i>Tryonia cf. scalarioides scalarioides</i>			1	
<i>Tryonia nuttalli</i>		1		
<i>Tryonia scalarioides scalarioides</i>		1		

## 5.5. Dinoflagellate biostratigraphy

Biostratigraphical analysis with dinoflagellate cysts and acritarchs is heavily influenced by facies and therefore can only be used as an accessory source of relative ages. The presence of some key taxa, however, indicates deposition during the early and middle Miocene, in accordance with pollen and mollusc ages. All identified dinoflagellates are listed and illustrated in Chapter 4. Comparisons are made with records of worldwide marine sequences where dinocysts are present.

The lowest marine interval (284 to 293.3 m) holds the marker dinoflagellate cysts species *Apteodinium? vescu*m (late Burdigalian to early Serravallian or N8-N11 in Matsuoka 1983), *Cleistosphaeridium ancyreum* (early Eocene to mid Miocene in Eaton *et al.* 2001), *Cleistosphaeridium placacanthum* (mid Eocene in Eaton *et al.* 2001 to early Tortonian, 10.6 Ma, in Schreck *et al.* 2012), *Quadrina “incerta”* (=Dinocyst XI of Lenoir and Hart 1986, late Burdigalian) and the acritarch *Quadrina? condita* (late Burdigalian in Soliman *et al.* 2012 to late Tortonian in de Verteuil 1996). These stratigraphic ranges infer deposition sometime between the late Burdigalian and the early Serravallian, i.e. late early Miocene to late middle Miocene. A late early Miocene is in agreement with pollen ages for the lower marine interval.

The deposition of the upper marine interval (101.2 to 96.7 m) took place sometime between the late Burdigalian and the early late Miocene (i.e. Tortonian) based on the stratigraphic ranges of *Quadrina? condita*, the rare dinocyst *Trinovantedinium? xylochoporum* (late Oligocene to Tortonian in de Verteuil 1996) and the acritarch *Cyclopsiella elliptica* (late Oligocene to early late Miocene in Matsuoka and Head 1992). These presences only give a rough estimate of age, but the absence of *C. ancyreum* and *C. placacanthum* as well as other gonyaulacacean dinoflagellate cysts in the upper marine sequence indicate it may be close to the top ranges of these taxa. In such case, the interval would be late Middle Miocene or younger, which is overall in agreement with the ages derived from graphic correlation. Late



Miocene and Pliocene dinocyst species are absent in the upper marine interval (S. Louwye *personal communication*).

## **5.6. Regional correlations (and the age of the Solimões Formation)**

Other localities in the Solimões Formation and surroundings (Fig. 5.7) where biostratigraphical data are available are herein used for correlation. This correlation aims to assess the total age range of the Formation and its geographical variations. The proposition of large scale paleogeographical models including specific events like fluvial migrations, marine incursions, etc, relies on a consistent biostratigraphical framework. Hence, a reappraisal of dated sequences basinwide is here offered based on the new studied section and its correlations with other sites.

Four cores in the same region as 105-AM were studied by Hoorn (1993), Latrubesse *et al.* (2007, 2010) and Silva-Caminha *et al.* (2010). Three of them reached similar depths to 105-AM (ca. 400 m) and had abundant pollen recovery. One section (32-AM, Latrubesse *et al.* 2010) only had its 133 top metres studied. Many other sections cropping out along rivers and road cuts were studied by Hoorn (1994a, 1994b, 2006), Latrubesse *et al.* (2010), Gross *et al.* (2011) and Nogueira *et al.* (2013), they are much shorter than the cores and have data on pollen and paleovertebrates. I attempted graphic correlation between cores 4a-AM and 27-AM (where longer stratigraphical ranges of taxa are possible), and more general correlations with the other localities using presence of key markers. Graphic correlation with core 32-AM was not performed due to its short range and therefore being completely dominated by edge effect.

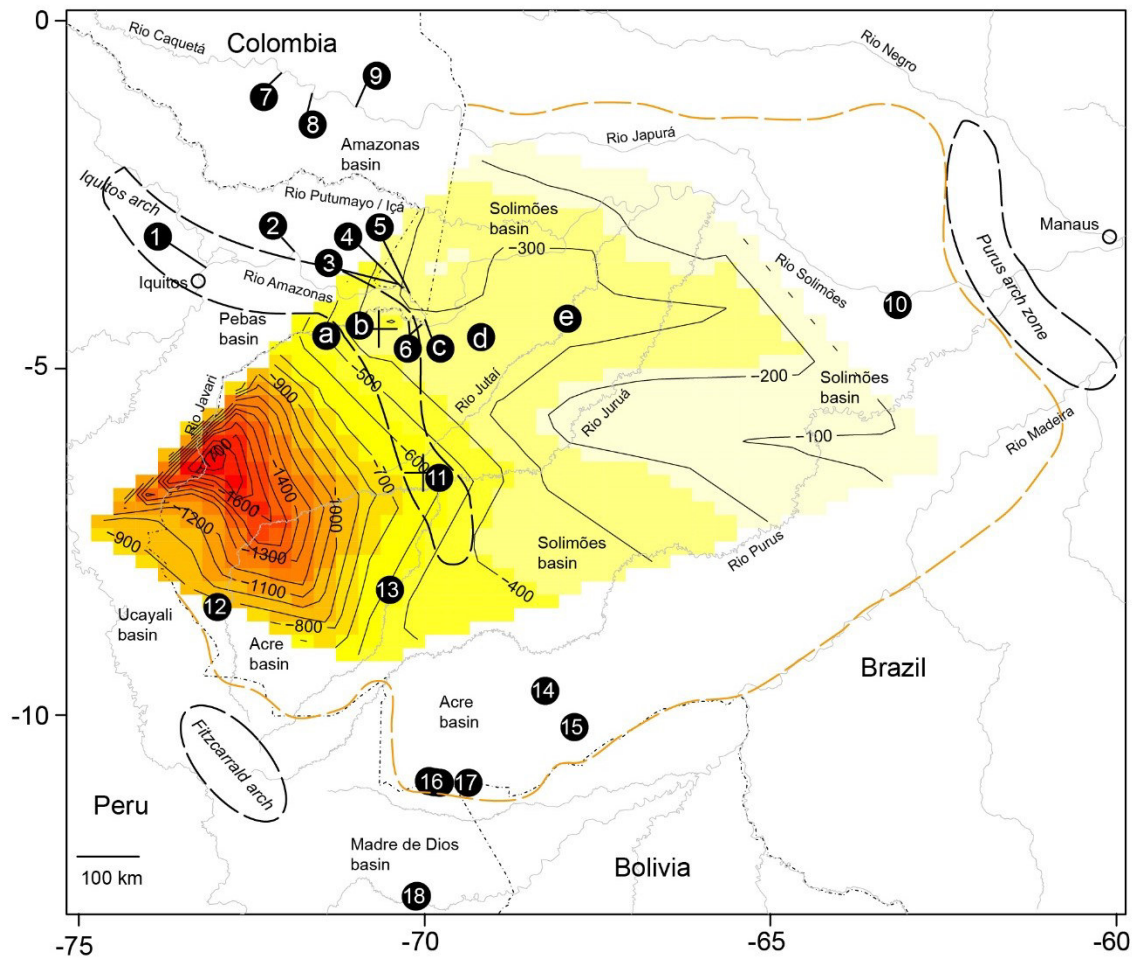


Fig. 5.7. Map showing the Solimões Formation sites discussed in the text and structural features in the area. Letters (a to e) are cores: a) 1-AS-32-AM, b) 1-AS-4a-AM (Hoorn 1993), c) **1-AS-105-AM (this work)**, d) and e) 1-AS-19-AM and 1-AS-27-AM, respectively (Silva-Caminha *et al.* 2010); numbers 1) to 9) are outcrops studied by Hoorn 1994a, 1994b: 1) Iquitos/Santa Teresa, 2) Pebas, 3) Los Chorrros, 4) Mocagua, 5) Santa Sofia, 6) Benjamin Constant, 7) Mariñame, 8) Santa Isabel, 9) Tres Islas, 10) Coari (Nogueira *et al.* 2013), 11) Eirunepé (Gross *et al.* 2011) and 12) to 18) outcrops studied by Latrubesse *et al.* (2010). Isopach lines were plotted using formation thickness measured in 107 boreholes, which includes sites a) to d), from the Brazilian Geological Survey (CPRM) and Petrobrás. Data was linearly interpolated using R package Akima. Positions of arches after Hoorn (1993), Roddaz *et al.* (2005) and Mora *et al.* (2010). Dashed orange outline is approximate limit of the Solimões Fm in Brazil. Crosses (+) are sites where the location of the Iquitos arch was determined by Miura (1972).

*Correlation 1-AS-105-AM vs. 1-AS-4a-AM (Hoorn 1993):*

Core 4a-AM was originally dated as early to middle-late Miocene by Hoorn (1993) based on presences of key markers *Crassoretitritiles vanraadshoovenii* and *Grimsdalea magnaclavata*. *C. vanraadshoovenii* appears at 181 m and *G. magnaclavata* at 89 m, both are frequent and abundant after their FADs. In core 105-AM *C. vanraadshoovenii* and *G. magnaclavata* appear at 361 and 326, respectively. Towards the top of section 4a-AM, *Retitricolpites lorentae* (= *Bombacacidites lorentae* nov. comb.) and *Multimarginites vanderhammenii* have the same FAD at 59 m, these species also have very similar FADs in section 105-AM, at 272.1 and 267.9, respectively. Because of these similarities in their sequence of appearances, all four species were chosen to compose the line of correlation. The result of this correlation (Fig. 5.8) shows that core 4a-AM is correlative with the bottom part of core 105-AM and correlates with the early Miocene. This result is similar to the original biostratigraphy of Hoorn (1993) but differs in that middle Miocene is not clearly evident in section 4a-AM. Middle Miocene had been established based on the *Grimsdalea* pollen zone (Lorente 1986) starting at 89 m. However, the FAD of this taxon is late early Miocene (Jaramillo *et al.* 2011, in prep) and given that only ca. 66 m of this range are present in 4a-AM it is possible no middle Miocene or very little of it is present. Other common middle Miocene taxa like *Ladakhipollenites? caribbiensis* and *Cichoreacidites longispinosus* which are frequent in 105-AM are completely lacking in 4a-AM. This further supports that core 4a-AM is older than 105-AM and may not extend into the middle Miocene.

The early Miocene marine flooding could be present in 4a-AM, but this is not certain as only rare indeterminate dinoflagellates were reported, therefore the flooding surface was not used in the correlation. In spite of that, the top of the supposed marine flooding is very close to the line of correlation (Fig. 5.8) showing a likely congruence of this event in both sections.

*Correlation 1-AS-105-AM vs. 1-AS-27-AM (Silva-Caminha et al. 2010):*

Silva-Caminha *et al.* (2010) studied two cores (1-AS-27-AM and 1-AS-19-AM) that were inter-correlated and appear to represent equal age ranges of late Miocene to early Pliocene. Correlation here is attempted with core 27-AM only. Core 19-AM was not used because it had just eight samples analysed as opposed to 33 of core 27-AM. A large edge effect is predominant in core 27-AM, this is clear when one looks at the many FADs lined up at the bottom of the section (Fig. 5.8). This hampered a reliable choice of where to place the line of correlation. Nevertheless, *C. longispinosus* and *Bombacacidites araracuarensis* were chosen as they have the same FAD in core 27-AM (354.5 m) and nearly the same in 105-AM (165.5 and 161.7 m, respectively) and they are frequent after their FAD. Furthermore, because these taxa have their FADs at ca. 160 m in 105-AM and they are basically present in the entire 27-AM section (from 354 m onwards), this means approximately 200 metres of displacement between the events from one section to the other, and hence 27-AM is younger than 105-AM. The top end of the line of correlation was tentatively set at the FAD of *Retitrescolpites? traversei*. This species is a singleton at 44.7 m in core 105-AM and has a FAD at 216 m in core 27-AM followed by two more presences until 137 m. The final correlation shows that 105-AM is older than 27-AM, and that a large proportion of the latter (ca. top 200 m) does not have a tie point. Assuming age assignments by Silva-Caminha *et al.* (2010), this top part of core 27-AM is late-Miocene to early Pliocene. However, no Pliocene marker was found to constraint this interpretation, in fact no late Miocene markers were found either, like *Cyatheacidites annulatus* that has a common presence in surface late Miocene regional outcrops (see section below). Hence, the topmost age of core 27-AM should be around the mid-late Miocene.

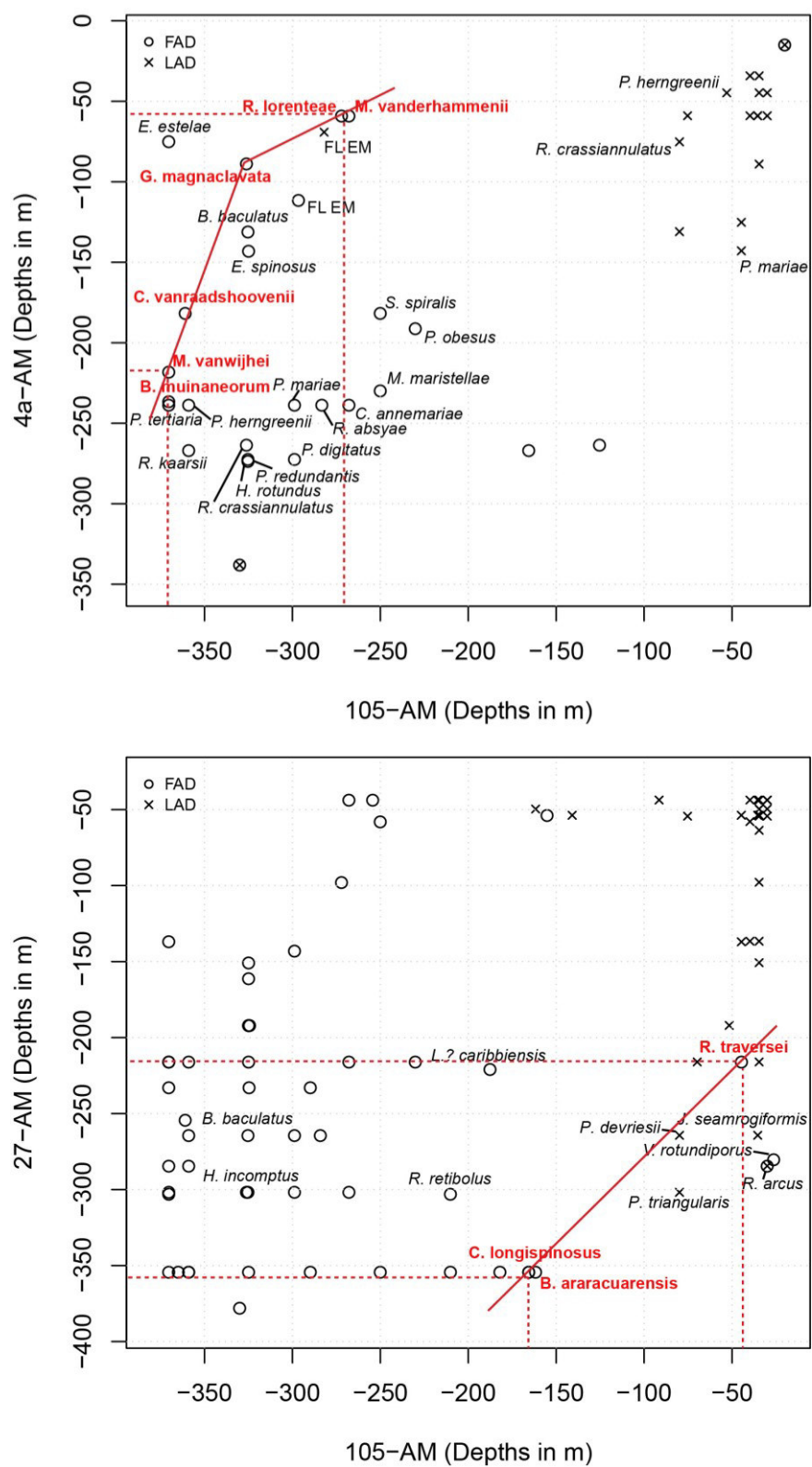


Fig. 5.8. Graphic correlation between cores 105-AM vs. 4a-AM (top), and 105-AM vs. 27-AM (bottom).

*Other localities:*

Core 32-AM (Latrubesse *et al.* 2010) was placed in the late Miocene-Pliocene Fenestrites zone (Lorente *et al.* 1986) based on the presence of *L.? caribbiensis*. However, as shown in the present study, this taxon first appears during the middle Miocene in western Amazonia. That and the lack of other late Miocene-Pliocene markers in core 32-AM makes it more plausible to correlate it with a middle-late Miocene age. It is uncertain how much this site extends into the late Miocene. The short depth (133 m) and the fact that the range of *L.? caribbiensis* can be of 187 and 221 metres in cores 105-AM and 27-AM, respectively, show it is possible that the entire core 32-AM is restricted to the middle Miocene. These uncertainties are probably due to the low number of samples (n=13, ~1 sample/10 metres) analysed in this core, thus more data is needed to better constrain its age.

Hoorn (1994a, 1994b) studied several outcrops in the Pebas and Amazonas basins as well as sections in Benjamin Constant/Atalaia do Norte area located between cores 4a-AM and 105-AM in the Solimões basin (Fig. 5.7). In Peru, the sections of Iquitos and Pebas yielded pollen assemblages containing *C. vanraadshoovenii* and lacking all other marker species including *G. magnaclavata*. This led Hoorn (1994a) to place the sections in the middle Miocene Crassoretitritetes pollen zone (Lorente 1986). However, as established by the correlation between 105-AM and the composite section, *C. vanraadshoovenii* like *G. magnaclavata* first appears in the late early Miocene. Thus, it can be deduced that the sections in Iquitos and Pebas area are early Miocene and do not extend into the middle Miocene. The absence of *G. magnaclavata* is quite indicative, because once this species appears it is usually very frequent and abundant. Also in this region is a 12 m long section (Santa Teresa) that does not even contain *C. vanraadshoovenii* and therefore can be attributed to the lower pollen zone Psiladiporites/Crototricolpites of early Miocene age (Lorente 1986). Hence, all sections of the Pebas basin in Peru are of early Miocene. In a more northerly

Amazonas basin of Colombia, three localities were also studied by Hoorn (1994b).

Mariñame, Santa Isabel and Tres Islas are outcrops of similar age to the Iquitos/Pebas sections as they do not contain any of the late early and middle Miocene marker taxa and thus they can be also attributed to the lower pollen zone *Psiladiporites/Crototricolpites* of early Miocene age (Lorente 1986).

The sections of Los Chorros, Mocagua, Santa Sofia (in Colombia) and Benjamin Constant and Atalaia do Norte (in Brazil) (Fig. 5.7) are younger as they contain *G. magnaclavata* apart from *C. vanraadshoovenii*. Hoorn (1994a, 1993) placed these sections in the middle Miocene Grimsdalea zone (Lorente 1986). As shown before, *G. magnaclavata* first appears in the late early Miocene, so it is possible these sections start at this age and extend into the middle Miocene as well. They cannot reach, however, a mid-middle Miocene age since markers common in the nearby cores 105-AM, 27-AM and 19-AM like *C. longispinosus* and *L.? caribbiensis* are completely absent.

Other sections in the Solimões Formation are outcrops in Eirunepé, Coari and various sites in the Acre/Madre de Dios basins (Fig. 5.7). In Eirunepé, Gross *et al.* (2011) reported the presence of *G. magnaclavata*, *Echitricolporites spinosus* and *Cyatheacidites annulatus* in two sections. While the first two taxa range from late early Miocene to Pliocene-Modern, *C. annulatus* has a FAD at 7 Ma (Jaramillo *et al.* 2011), henceforth constraining the age of Eirunepé sections to not older than a late late Miocene stage. In Coari (Nogueira *et al.* 2013), six sections yielded a similar pollen assemblage to Eirunepé's, with *C. annulatus* suggesting a late late Miocene age as well, and *Ladakhipollenites? caribbiensis* and *Stephanocolpites evansii* suggesting late Miocene (Lorente 1986, Jaramillo *et al.* 2011). These sections in Coari are unconformably overlain by the Içá Formation of Pleistocene age. There is no age for the unconformity, but the continuity of the late late Miocene (7 Ma or younger) towards the Pleistocene suggests that the Pliocene is possibly also present in the region. Many authors

have suggested that the upper Solimões Formation extends to the Pliocene (Latrubesse *et al.* 2010, Silva-Caminha *et al.* 2010, Nogueira *et al.* 2013) based on pollen and mammalian biozones. This needs further study since no definitive Pliocene marker fossils have been established in the region.

In the Acre basin several outcrops (Fig. 5.7) were studied by Latrubesse *et al.* (2010) and Cozzuol (2006). Extensive vertebrate palaeontology and additional palynology analysis place the outcrops in the Huayquerian–Mesopotamian mammalian biozones, which ranges from 9 to 6.5 Ma, hence of late Miocene age.

Other outcrops in the Solimões basin region as well as cores from the ‘Solimões Coal project’ (CPRM) were studied by Cruz (1984). Unfortunately the pollen data and spatial distribution of sites is not available in the publication. Nevertheless, some interesting insights can be drawn from this work. The report of an association (zone A, Cruz 1984) containing *Cicatricosisporites dorogensis* and completely lacking other late early and middle Miocene markers indicates the existence of Oligocene or earliest early Miocene sediments, most likely among the bottom parts of cores. *C. dorogensis* is known to go extinct at the Oligocene–Miocene boundary (Regali *et al.* 1974, Lorente 1986, Jaramillo *et al.* 2011). Associations B–C established by Cruz (1984) contain *C. vandraashoovenii*, *E. spinosus*, *G. magnaclavata*, *F. spinosus*, *Retistephanocolpites gracilis* and *C. annulatus* pointing to middle to late Miocene ages (Germeraad *et al.* 1968, Regali *et al.* 1974). Although lacking detailed description of data and samples, Cruz (1984) found late late Miocene to Pliocene beds of sediments are correlatable with those in Eirunepé and Coari based on the presence of *C. annulatus*.

In sum, the Solimões Formation exhibits sediments from early Miocene (ca. 20 Ma) to late Miocene (6.5 Ma). Early Pliocene seems to be present at the eastern parts of the basin (at Coari), a broader extension of Pliocene is possible but needs further testing. Late Oligocene is probable, but further confirmation is needed.



Regarding the possibility of a Pliocene age for the topmost Solimões Formation, a few considerations must be made. First, as exposed above the few metres of sections basinwide in the *C. annulatus* Late Miocene zone ( $\leq 7$  Ma) could naturally extend into the Pliocene. The *C. annulatus* zone extends into the Pliocene and the taxon is present in the Quaternary as well. Second, in other parts of western Amazonia there are good clues on when the Solimões Formation ceased to accumulate sediments. That is the case of the Acre/Madre de Dios basins. In that region, an important feature controlling watersheds is the Fitzcarrald arch in Peru (Fig. 5.7). It splits apart the Ucayali and the Madre de Dios basins, thus creating the southern limit for the Amazon drainage (Mora *et al* 2010, Latrubesse *et al.* 2010). The Fitzcarrald arch uplifted as a result of a flat slab subduction of the Nazca Ridge, which is dated as Pliocene, to approximately 4 Ma (Espurt *et al.* 2007, 2010). This event lead to the termination of deposition and the initiation of an erosional phase in SW Amazonia. Therefore, if this assumption is correct, the upper Solimões Formation in the region can reach an early Pliocene age. Moreover, assuming a lag between the Fitzcarrald emergence and a full fluvial migration towards eastern Solimões Basin, the upper Solimões Formation in central Amazonia (Coari) could very reasonably be of mid to late Pliocene. This interpretation can reconcile uncertainties regarding the upper Solimões Formation and demonstrate a synchronous depositional phase over an immense geographical area (Fitzcarrald and Coari are ca. 1,200 km apart) as proposed by Latrubesse *et al.* (2010) and Nogueira *et al.* (2013).

A clear pattern among the cores was found – older ages westward and younger ages eastward (Fig. 5.9). This pattern is similar to the overall spatial configuration of the Solimões Formation deposits, which thin out from SW to NE (Fig. 5.7, Maia *et al.* 1977, Latrubesse *et al.* 2010). However, further explanations are necessary to contend this age differences among cores so closely spaced. One idea is that the Iquitos Arch was active and affected

sedimentation in this area during the Miocene (, Latrubesse *et al.* 2007, 2010, Silva-Caminha *et al.* 2010). The Iquitos Arch is the product of a flexural forebulge uplift (Roddaz *et al.* 2005) related to Andean tectonics. Tectono-sedimentary evidences suggests a late Miocene timing for the forebulge growth (Roddaz *et al.* 2005), which coincides with accelerated rates of mountain build in the Andes (Hoorn *et al.* 2010) that in turn is the primary driver of forebulge dynamics. The position of the Iquitos arch was determined by gravimetric anomalies showing strong positive Bouguer values around the Iquitos town in Peru (Roddaz *et al.* 2005) and close to core 4a-AM and the town of Eirunepé in Brazil (Miura 1972) (Fig. 5.7). It is not clear how much of this feature extends in other directions regionally. Assuming the proposed Late Miocene as a time of arch activity, its role could have been to promote exhumation of older sediments rather than influencing their deposition. This would explain the outcrops in the Pebas and Solimões basins studied by Hoorn (1994a, 1994b, Fig. 5.7, Fig. 5.8) which have early to early middle Miocene ages contrasting with other late Miocene outcrops in other areas (e.g. Coari, Eirunepé). Interestingly, other structures in NW Amazonia are hypothesised to have emerged during the late Miocene-Pliocene like the Vaupés Swell in Colombia (Mora *et al.* 2010) (Fig.1.2). Indeed, some authors (Wesselingh and Salo 2006, Wesselingh 2008) pointed to the difficulties in delineating such subsurface structures and prefer to unite all evidences of uplifts in the Amazonas basin (Colombia) and call it the Iquitos-Araracuara anteklise, a post-Pebasian (late Miocene) broad dome. With this assumption, tectonic activity in the NW Solimões/Pebas/Amazonas basins (Fig. 5.7) during the late Miocene would be the responsible for the discrepancies in outcrop ages seen between this region and elsewhere in the basin.

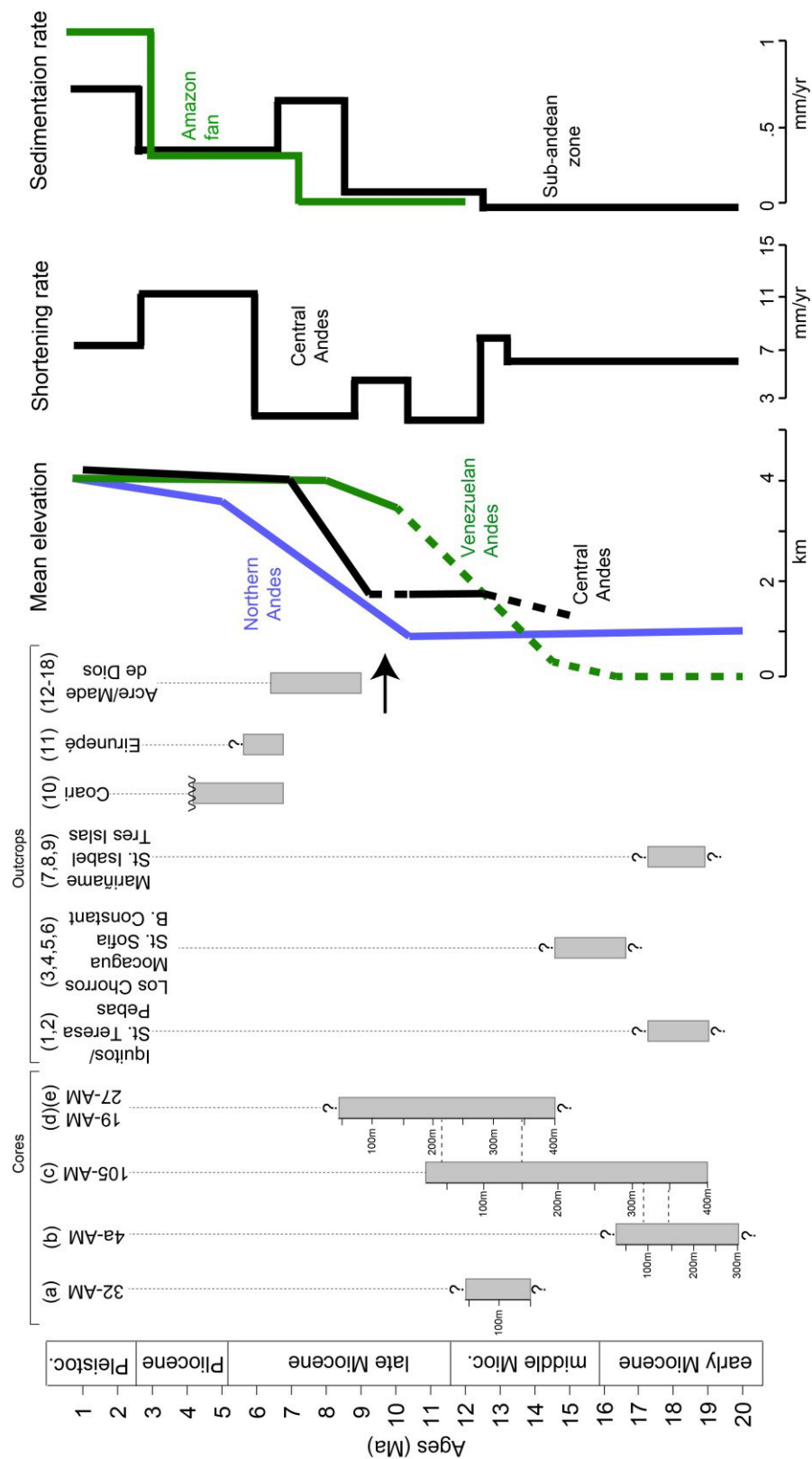


Fig. 5.9. Correlation among sites in the Solimões/Amazonas/Pebas/Acre/Madre de Dios basins (for locations see Fig. 5.6). Schematic representation of Mean elevation, shortening and sedimentation in different parts of the Andes are shown (adapted from Hoorn *et al.* 2010), arrow points to late Miocene periods when uplift was pronounced and affected the landscape in western Amazonia by promoting deformation (e.g. Iquitos arch, see text for details).

## **Chapter 6: Palaeoenvironments in western Amazonia during the late Early to early Late Miocene: evidence from palynology of core 1-AS-105-AM (Solimões Formation)**

### **6.1. Introduction**

Amazonia underwent profound landscape changes during the Miocene. Prior to the late Miocene, the Amazon River was split in two with one branch running westward (Figueiredo *et al.* 2009, Hoorn *et al.* 2010). Central Amazonia cratonic areas, as well as the Andes, were drained by rivers that discharged into an immense wetland system that developed during the early, middle and early late Miocene in western Amazonia (Hoorn 1993, Wesselingh *et al.* 2002). This system, often referred to as the Pebas system (or lake), comprised a series of lakes, megalakes, rivers, deltas, estuaries, and floodplains much like the Pantanal of central Brazil, Paraguay and Bolivia are at the present time, but at a much larger spatial scale. When at its full development as a lake, estimates put this system to over one million km<sup>2</sup> in extension, making it one of the largest ever recorded lakes (Wesselingh *et al.* 2002, Wesselingh 2007, 2008). The Andean uplift during the Miocene is a heavy influence on the evolution of the Pebas system. Mountain building created continuous accommodation space in the forelands. This and the lack of other significant relief in western Amazonia resulted in a low gradient and low energy scenario suitable for the development of wetlands. Prior to late Miocene and Pliocene, when Andean tectonism was the strongest and caused most deformation in the foreland basins, important watersheds did not exist (Mora *et al.* 2010). This signifies that the outline of western Amazonia as a whole was larger, extending south into the central Andes in Bolivia, and north through the Llanos basin in Colombia into the Orinoco basin. This Pan-Amazonia area had a long-lived interconnectedness, so much so that episodes of marine incursions are detected from the Caribbean to southwest Amazonia (Hoorn *et al.* 2010, Antoine *et al.* 2016), approximately 2,500 km distant from each other.

The marine incursions into western Amazonia are probably the most debated topic in the Amazon literature (see for instance Latrubesse *et al.* 2010). Their existence is suggested since early works on molluscs from the area (Gabb 1869, Woodward 1871, Boettger 1878). Shells with affinities to North American and Caribbean taxa were indicative of marine connections. This fossil record plus sedimentary characteristics lead authors already in the early twentieth century to postulate inundation theories for the upper Cenozoic in western Amazonia that would only decades later be confirmed. One author wrote that, “the Tertiary rocks appear from their characters and fossils to be of fluvial, or possibly brackish-water, origin. (...) The rise of the Andes would dam up the ancient [Amazon] river into a lake which would eventually find an outlet eastward, as at present” (Sherlock 1934, pages 115-116). Later, in the early 1950s, T. Van der Hammen in his initial works in Colombia saw wide extensions of sediments with iron oölite and manganite, indicating presence of lacustrine and brackish-water conditions. These were years later confirmed by his finding of mangrove pollen (*Zonocostites*) in Neogene sediments. Finally, in the early 1990s a more refined picture emerged with the studies of Nuttal (1990) and Hoorn (1993, 1994a, 1994b) who dated more precisely sediments of western Amazonia to the Miocene.

Existence of marine indicators in western Amazonia early and middle Miocene beds is irrefutable. Among the most compelling fossils with marine affinities include: molluscs, foraminifera (tests and linings), dinoflagellate cysts (dinocysts), ostracods (*Cyprideis*), bryozoans, decapoda, fish teeth (shark, stingray, sawfish), sea urchins and various ichnofossils (Lorente 1986, Dueñas 1980, Hoorn 1990, 1993, 1994a, 1994b, Monsch 1998, Rull 2001, Wesselingh *et al.* 2002, Salas-Gismondi *et al.* 2006, Antoine *et al.* 2007, 2016, Hovikoski *et al.* 2007, 2010, Bayona *et al.* 2007, Linhares *et al.* 2011, Bianucci *et al.* 2013, Boonstra *et al.* 2015). Other than fossils, strontium isotopes from molluscs (Vonhof *et al.* 1998, 2003), molecular data of Amazon fish with relatives in the Caribbean (Lovejoy *et al.*

1998, 2006, Cooke *et al.* 2012) and preserved tidal sedimentary structures (Hoorn 1994a, Hovikoski *et al.* 2007, 2010) further point to marine connections. Despite this body of evidence, there are still some contentious topics and many unanswered questions in the literature. First, what was the timing, duration and significance of marine incursions? The chronostratigraphic framework used in western Amazonia relies heavily on palynology of the Solimões and Pebas Formations. Pollen zones adapted from Venezuela (Lorente 1986) are used and also served to aid the formulation of other biostratigraphic frameworks like the molluscan zonation of Wesselingh *et al.* (2006a). Such zones are best estimates but do not provide a high temporal resolution to bracket specific events. Furthermore, the great majority of studied sites are outcrops. Because (i) the beds of the Solimões/Pebas and adjacent deposits lie horizontally or sub-horizontally, (ii) the overall landscape is flat and (iii) there is a dense forest cover, exposed sections cannot cover long vertical ranges. These factors, and the lack of good age control, mean basinwide correlations are rendered difficult. Second, what was the geographical extension of the marine incursions? This question, in turn, is directly linked to the first question because age correlation is essential to map spatial and temporal distribution of a given inundation event.

Another issue, which is perhaps the least tested of all, is to what extent these inundations affected the forest structure and composition. Some authors have used the flooding dynamics (flood x dry) to inform theories about biodiversity (Nores 1999, 2004). Large scale inundations potentially create countless islands on high ground that isolated fauna and flora and encouraged allopatric speciation (Nores 1999, 2004). They also allegedly gave rise to novel environments like mangroves and estuaries of variable salinities. If this all is true, we should be able to detect some signal of species changes related to such events. To test some of the questions contended above, a paleoenvironmental analysis was carried out using the pollen data generated from core 1-AS-105-AM. Palynomorphs were grouped in

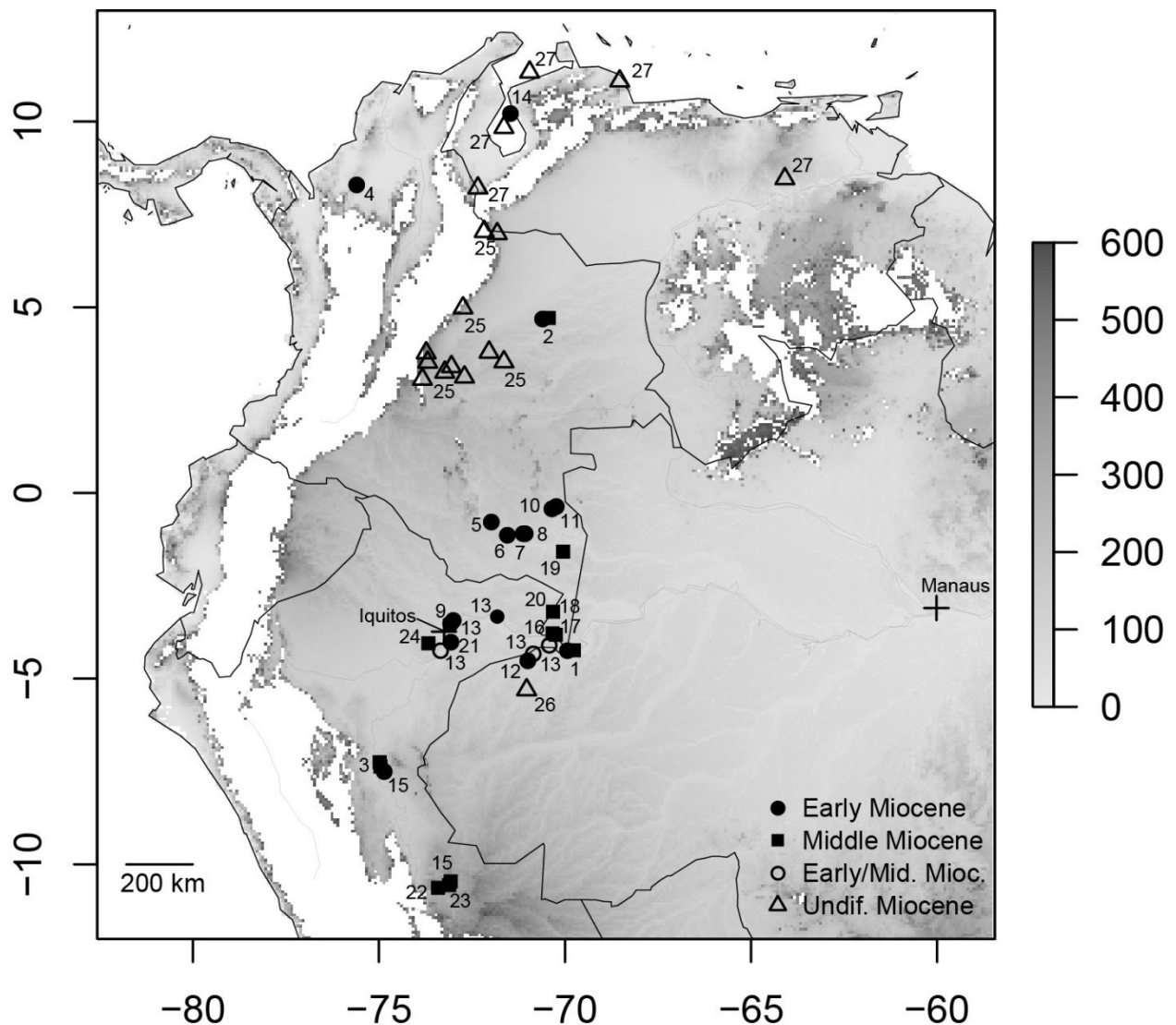


Figure 6.1. Location map of sites where marine incursions have been evidenced by fossils: **1 (core 105-AM, this study)**, 2 (core Saltarin, Jaramillo *et al.* in prep), 3 (Contamana, Antoine *et al.* 2016), 4 (core Q-E-22, Dueñas 1980, Bayona *et al.* 2007), 5 to 8 (various outcrops in Mariñame, Hoorn 1990, 1994b), 9 (outcrop Santa Teresa, Hoorn 1994a), 10 and 11 (outcrops in Apaporis, Hoorn 2006), 12 (core 4a-AM, Hoorn 1993, Vonhof *et al.* 2003), 13 (various outcrops by Hovikoski *et al.* 2005, 2007, 2010), 14 (core Tj, Rull 2001), 15 (sites revisited by Boonstra *et al.* 2015, see text for details), 16 to 20 (various outcrops studied by Hoorn 1994a, 1994b, Wesselingh *et al.* 2002, Vonhof *et al.* 2003), 21 (Loreto locality IQ-115, Monsch 1998, Boonstra *et al.* 2015), 23 and 23 (Fitzcarrald area, Salas-Gismondi *et al.* 2006, Antoine *et al.* 2007, Bianucci *et al.* 2013, Boonstra *et al.* 2015), 24 (Loreto locality N. Horizonte, Wesselingh *et al.* 2002, Vonhof *et al.* 2003), 25 (various cores studies by Bayona *et al.* 2007), 26 (core 33-AM, Linhares *et al.* 2011), 27 (various localities studies by Lorente 1986).

their ecological and botanical affinities, contrasted against the age estimated for the core and finally compared to other published localities. The full methods can be found in Chapter 3.

## 6.2. Results

### *Marine incursions*

Two conspicuous marine levels were detected in core 105-AM (Fig. 6.2 and Fig. 6.3). They were established on the basis of peak abundances of dinocysts, foraminiferal linings and mangrove pollen (*Zonocostites* + *Lanagiopollis crassa*). The lower incursion (MF1) took place from ca. 18.4 to 17.8 Ma (duration of 0.57 Ma). The maximum extent of marine flooding is at the top of the interval with a 200,000 yrs period from 17.83 to 18.03 revealed by an abundant and rich dinocyst assemblage. At the bottom of MF1 dinocysts are rare ( $\leq 1\%$ ) but a peak in foraminiferal linings and *Zonocostites* is present. Between the bottom and top of MF1, gaps exist of up to ca. 0.02 Ma (but potentially 0.1 Ma) where samples contain no marine indicators. The upper marine incursion (MF2) took place from ca. 14.10 to 13.73 Ma (duration of 0.37 Ma). It is expressed by spikes in dinocyst and one rare occurrence of an undetermined foraminifera at ca. 98 m or ca. 13.8 Ma (Fig. 6.3), which coincides with the highest dinocyst abundance peak. MF2 also has a gap where no marine evidence was recorded, but estimating its duration is not possible because it is covered by only one sample. Twenty one dinocyst taxa were recorded in total, 14 of which have identification to the species level (Fig. 6.3 and plates 26-27 of Chapter 5). Dinocyst abundance data are distributed in all types of lithologies with no significant differences found (Kruskal-Wallis one way Anova;  $K=1.5121$ ,  $p=0.6795$ ). However, dinocyst peak abundances ( $>40\%$ ) are restricted to mudstones (Fig. 6.4), thus suggesting marine incursions occurred during periods of lake development, probably at peak megalake stages when the water table was high throughout the basin.



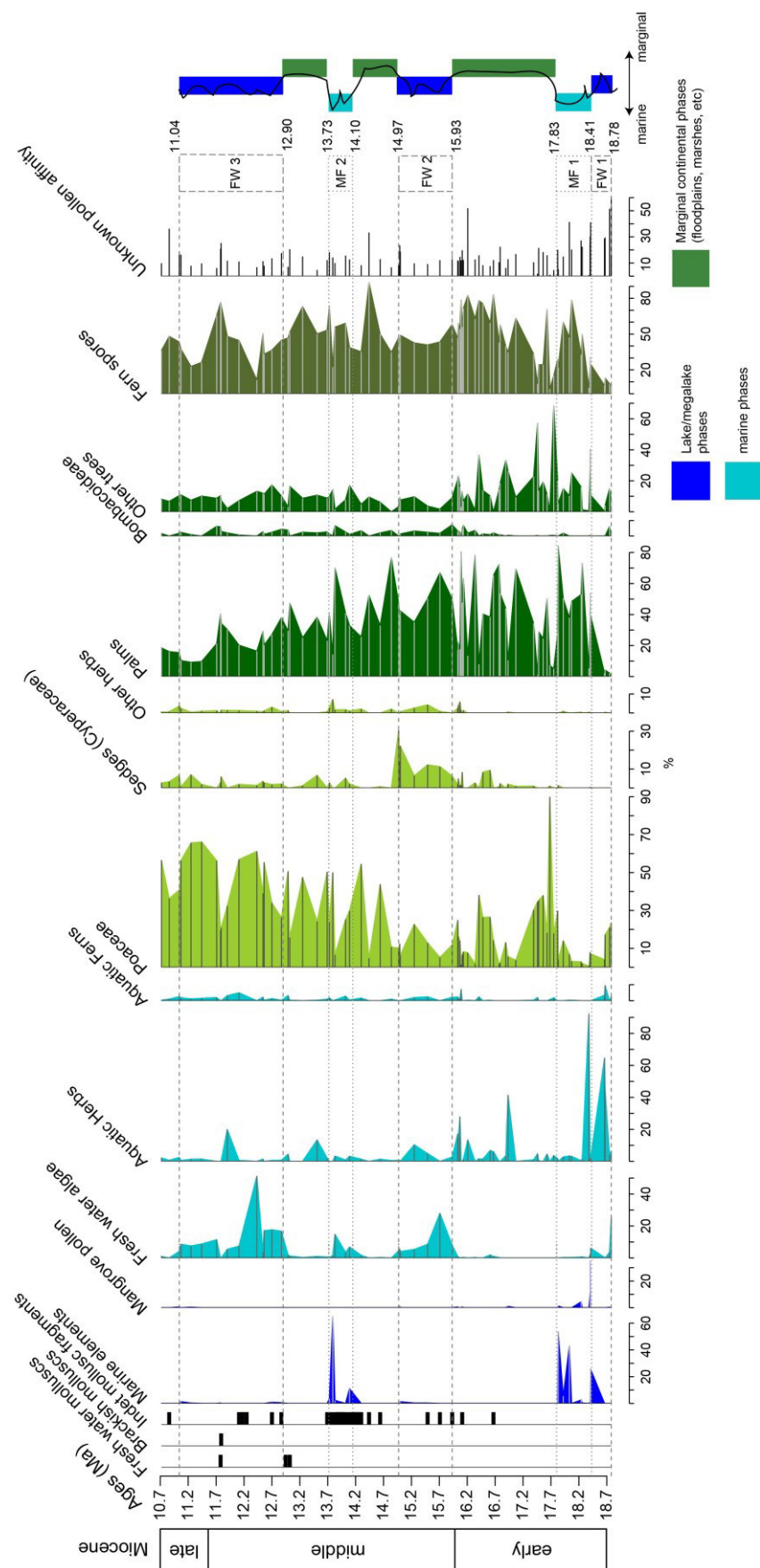


Figure 6.2. Summary percentage diagram of ecological groups. Solid line along the coloured bars represents empirical interpretation of variability in the changing environmental settings.

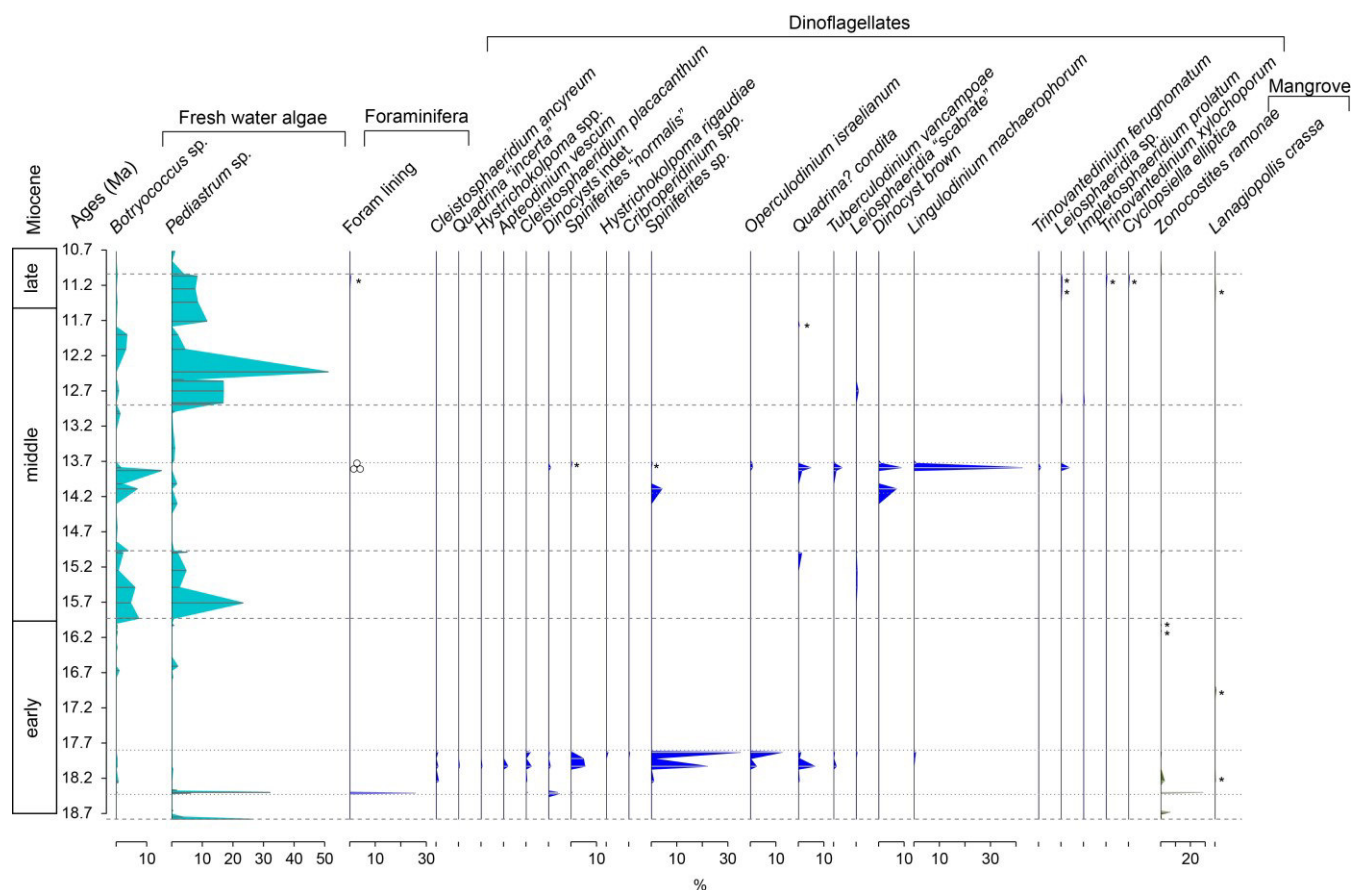


Figure 6.3. Freshwater and marine water indicators, including all dinocyst taxa identified. Rare occurrences ( $\leq 1\%$ ) are highlighted with a “\*”. Notice foraminifera symbol at ca. 13.8 Ma ( $\otimes$ ).

### *Fresh and brackish water phases*

Whereas clear marine inundations are evident from peak dinocyst abundance (MF1 and MF2), freshwater-dominated phases with occasional brackish conditions also existed. These fresh water phases are spread in three different periods - at the base of the 105-AM sequence (FW1, from 18.78 to 18.41 Ma), at the middle (FW2, from 15.93 to 14.97 Ma) and in the upper part (FW3, from 12.90 to 11.04 Ma). They were established after the continued and abundant presence of fresh water algal cells *Pediastrum* spp and *Botryococcus* spp. These algae are present in all lithologies but in varying quantities, being more abundant in silts and sands (Fig. 6.4). In lignites, significantly less algae were recorded (Kruskal-Wallis one way Anova;  $K=14.37$ ,  $df=3$ ,  $p=0.00244$ ; and Post-hoc Tukey test: lignite vs. sand,  $p=0.0084$  |

lignite vs. silt,  $p=0.0255$ ). Further support of such lacustrine conditions can be indicated by peaks in aquatic plants pollen (Fig. 6.2) and mollusc taxa found at two levels (Fig. 6.2).

Among the mollusc species, *Charadreon*, *Aylacostoma* and *Sheppardiconcha* can be assigned to fluvial or marginal lacustrine ecologies, whereas all other species are Pebasian endemics (Wesselingh *et al.* 2002, Wesselingh 2006) and therefore most likely lacustrine. These include a few informal species from the Benjamin Constant fauna (F. Wesselingh *personal comm.*) A full list of mollusc species can be found in Chapter 5, Table 5.2. Also typical of fresh water flooding, like extant *várzeas* and *igapós*, is Bombacoideae (Bombax trees) with abundant palms.

During FW2 and FW3, rare occurrences of dinocysts point to brackish conditions. Although they are Neogene, moderately well-preserved dinocysts, they could still be reworked since the likely short distance from source to deposition would prevent them from being too damaged. However, at least during MF3, brackish conditions are also supported by the occurrence of brackish water bivalve species *Corbula cotuhensis* (Wesselingh 2006a) at 11.79 Ma (Fig. 6.2) and by the accumulation of carbonate mud (micrite) in thin different levels of the core (Fig. 2.1 and Appendix 9.4). These thin micritic bands can be produced by brackish conditions in an overall freshwater environment common in humid regions (Kelts and Hsü 1978). Calcareous sources could be layers of shells accumulated in lakes, calcareous algal blooms or inorganic inputs from detrital re-deposition. These scenarios could be related to freshwater carbonate accumulation only, like it has been reported in late Miocene Solimões Formation floodplain lakes rich in shells and other fossils (Gross *et al.* 2011). However, the presence of rare dinocysts and brackish bivalves strongly suggests transient fresh-brackish water dynamics during FW2 and FW3.

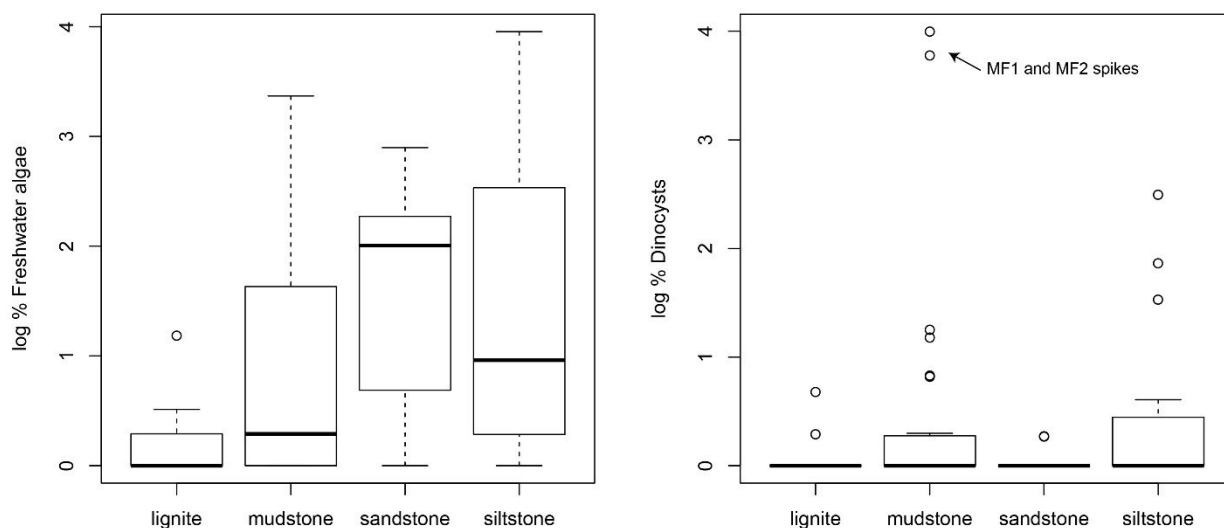


Figure 6.4. Abundance distribution of freshwater algae in comparison to lithology.

### Vegetation

Vegetation throughout the entire 105-AM core is typical of Amazonian lowland forests. The extant botanical affinities of fossil pollen, and their ecological significance, was compiled from the literature (see Appendix table 9.2). Of the total pollen species (fern spores excluded), 31.8% had known affinities at least to the family level. When reviewed in terms of abundance, 83% of the pollen counts had a known systematic affinity (Fig. 6.2). Among the most abundant families (Fig. 6.2) are grasses (Poaceae), palms (Arecaceae), Malvaceae (subfamily Bombacoideae), Euphorbiaceae, Melastomataceae, and Alismataceae (Fig. 6.5.). Except grasses and aquatic/swamp species (Alismataceae, Cyperaceae, Polygalaceae Onagraceae), the overall majority of plants belong to arboreal taxa. The dominance of palms, grasses, aquatic plants, a rich tree assemblage including seasonally flooded forest taxa (Bombacoideae, although not exclusively) as well as abundant ferns, is indicative of floodplains, swamps and *terra firme* forests. Thus, the pollen record points to the constant presence of warm and humid conditions. The presence of Podocarpaceae (*Podocarpus* sp)



and Loranthaceae (*Hedyosmum* sp.) could indicate either montane (Andean) sourced pollen carried by rivers or lowland montane-like plant communities in oligotrophic or water-logged soils (Householder *et al.* 2015, Punyasena *et al.* 2011, *personal observation*). *Hedyosmum* sp. invaded South America in the early Miocene, inhabiting lowlands (Martinez *et al.* 2013) during this time. Lineages of lowland tropical *Podocarpus* sp. emerged during warm Tertiary times (Quiroga *et al.* 2015), thus the presence of both taxa in lowland deposits does not necessarily reflect descent from Andean forests.

To test the possible effects of inundations (freshwater/brackish or marine) on the vegetation, a Canonical Correspondence Analysis (CCA) was run on the vegetation data set (species matrix). Environmental variables used for this were the presence of lake conditions (FW1, FW2 and FW3) and marine incursions (MF1 and MF2). Table 6.1 summarises the results of the CCA. *Constrained* CCA is the analysis that used the explanatory variables and *unconstrained* CCA is a correspondence analysis of the residuals of the constrained CCA. Only 3.78% of the inertia is explainable variation, whereas 96.21% is residual. The vegetation matrix transformed into binary data yielded very similar results (Table 6.1., shown in parenthesis). Therefore, nearly no effect on the abundance distribution or composition of plants is explained by the inundations. CCA axis scores (eigenvalues) weigh more on the Fresh/Brackish water inundation (71.4% of variation) than they did on Marine water (28.6%), further showing marine incursions have negligible effects on the vegetation. These axis scores will not be further explored due to the very poor fit of the analysis.

Table 6.1. Summary results of the Canonical Correspondence Analysis (CCA) of vegetation data against environmental variables (fresh/brackish and marine water).

	<b>Inertia</b>	<b>Proportion</b>	<b>Rank</b>
<b>Total</b>	3.81044 (4.38858)	100%	--
<b>Constrained</b>	0.14418 (0.14698)	3.78% (3.34%)	2
<b>Unconstrained</b>	3.66626 (4.24160)	96.21% (96.65%)	72

cca(formula = veg ~ FreshWater + MarineWater, data = environ); Inertia is mean squared contingency coefficient (to show how good the analysis was). Numbers in parenthesis are CCA run with binary matrix.

### 6.3. Discussion

#### *Dinocysts ecology and the nature of western Amazonian inundations*

The dinoflagellate cysts found here are commonly seen in a number of Neogene marine sequences worldwide and thus their niche occupancy can be interpreted. The majority of identified species from both marine intervals are neritic, cosmopolitan and with a broad tolerance for temperature (see below). No characteristic oceanic species are present. Only *Operculodinium israelianum* and *Tuberculodinium vancampoe* are restricted to subtropical, tropical and equatorial realm, favouring nearshore or coastal areas (Zonneveld *et al.* 2013). The upper marine incursion (MF2) has a spike of *Lingulodinium machaerophorum* (Fig. 6.3), this cyst is euryhaline and tends to attain high abundance in estuaries or in areas of coastal upwelling (Dale 1996). In the upper freshwater/brackish phase, at ca. 11 Ma, *Cyclopsiella elliptica/granosa* complex was recorded in a cluster. This species often form colonial biocoenosis (de Verteuil and Norris 1996), which points to an attached or perhaps encrusted mode of life (Matsuoka and Head 1980) in nearshore, high energetic environments (Louwye and Laga 2008). At the same sample, *Trinovantedinium xylocophorum* was recorded, this species as well as ‘rounded brown cysts’ (RBCs) of indeterminate Protoperidiniaceae affinity in MF2 is nonphotosynthetic or heterotrophic (Fensome *et al.* 1993). The same goes for *T.*

*ferugnomatum* present in MF2. The presence of these protoperidiniacean cysts and especially their considerable abundance in MF2 (Fig. 6.3) can be associated with enhanced nutrient levels driven by fluvial/deltaic input (Dale 1996). For instance, some protoperidiniacean dominated dinocyst assemblages are documented from the Oligocene of Nigeria (Biffi and Grignani 1983) and the Miocene of the Gulf of Mexico (Duffield and Stein 1986), both localities receiving high nutrient inputs from the Niger Delta and Mississippi delta complex respectively.

The acritarch species *Quadrina? condita* is present in both marine intervals and outside of them as well. Its ecology is still poorly understood but occurrences are seen in warm settings like lower to middle Miocene of the Gulf of Suez (Soliman *et al.* 2012) and productive shallow marine environments of middle to upper Miocene age in the Maryland-Virginia coast (de Verteuil and Norris 1996). Many of the individuals of *Q.? condita* seen in core 105-AM had a distinctive cruciform shape that is stronger than the original cruciform outline caused by spines being clustered at the corners of the cyst (see Figure 2 in Plate 27, Chapter 4). Cruciform shape has been shown to be the result of low salinity adaptation in many dinoflagellate species (Wall *et al.* 1973, Kouli *et al.* 2001, Mudie *et al.* 2001, Marret *et al.* 2004). This could be the case of *Q.? condita* as well since it is recorded in brackish waters in the Pebas system. Other species do not show signs of cruciform shape.

The lower marine interval (MF1) is dominated by *Spiniferites* species (Fig. 6.3). Unfortunately they could not be identified to the species level. The genus is cosmopolitan (Zonneveld *et al.* 2013), occupying open oceans and coastal regions from all latitudes, thus an ecological assignment to the *Spiniferites* assemblage in MF1 is imprecise. Other dinocysts in this assemblage are more informative, like *O. israelianum* and *T. vancampoe* that tend to be restricted to sub-(tropical) and equatorial nearshore and coastal regions (Zonneveld *et al.* 2013). Therefore, dinoflagellate ecology in both marine incursions is similar and indicative of



nearshore, shallow marine to estuaries, with high energy and high nutrient input in an equatorial setting.

#### *Freshwater/brackish phases*

Lake phases were established based on the abundant and consecutive presence of freshwater algae. This interpretation was based essentially on the green alga *Pediastrum* and done at the generic level, given the difficulties in identification of this polymorphic genus (Komárék and Jankovská 2001). *Pediastrum* is representative of low energy environments (Weiler 1985) like lakes. A number of studies have linked *Pediastrum* concentrations to lake level and temperature in the tropics (Rull *et al.* 2008, Gosling *et al.* 2008, Whitney and Mayle 2012). Different species of the genus can have contrasting water level and other ecological preferences (Komárék and Jankovská 2001). For instance, Whitney and Mayle (2012) studying lowland wetlands in central South America found that some taxa prefer deeper waters while others develop better in shallow water associated with a dense macrophyte cover. In core 105-AM, no relation was found between the relative abundance of aquatic plants and freshwater algae ( $r^2 = -0.010$ ,  $p = 0.667$ ), and therefore a preference of *Pediastrum* to very shallow water like ponds, marshes and bogs where the aquatic plants identified here thrive cannot be suggested. This agrees with the significant lower concentrations of algae in lignite facies (Fig. 6.4, see results), that are deposited in peat forming marshes and bogs. Hence, for the best of our knowledge, *Pediastrum* is pointing to lacustrine environments with a higher water table. This explains the higher amount of algae in coarser facies (Fig. 6.4, see results), that although they do not represent lake deposits (muds), they attest to connection of separate lacustrine systems by the action of avulsion, internal deltas and splays. Evidence of this connection is the occurrence of dinocysts during overall freshwater phases (FW2 and FW3) and full marine phases disrupting what was otherwise freshwater lakes. Full marine

phases are associated with mud facies, when lakes were at high stands and thus covered a wider geographical area.

*Comparison with other regional dinocyst records:*

*(1) Amazonas/Pebas/Solimões basins (sites 5, 6, 10, 16, 17, 18 and 20, in Fig. 6.1)*

The early to middle Miocene outcrops of Mariñame, Tres Islas, Apaporis, Los Chorros, Mocagua and Buenos Aires that are all in the southern Colombian Amazon were originally studied by Hoorn (1990, 1994a, 1994b, 2006) and recently revisited by Boonstra *et al.* (2015). They report low counts of dinocysts ranging from 1 to 35 individuals (0.3 to 11.6% of a typical 300 pollen count) what is in contrast with the high percentages attained in the full marine incursions reported herein (>40 % of the total count). Four dinocyst taxa are shared in both studies, *Spiniferites* spp, *T. vancampoe*, *Quadrina? condita* and indeterminate RBCs (Protoperidinioid). In addition, Boonstra *et al.* (2015) report *Polysphaeridium zoharyi*, *Brigantedinium* spp. and *Lejeunecysta* spp. *P. zoharyi* is found in subtropical, tropical to equatorial coastal sites (Zonneveld *et al.* 2013) and can be associated with lagoons and estuaries (Wall *et al.* 1977, Marret and Zonneveld 2003). The Protoperidinioids *Brigantedinium* spp. and *Lejeunecysta* spp. are heterotrophic cosmopolitan taxa and their abundance can be associated to high productivity (Zonneveld *et al.* 2013). Altogether, the dinocyst assemblages from 105-AM and the Hoorn outcrops point to the very similar environmental conditions of shallow marine, high-nutrient, and coastal areas.

In addition to dinocysts, Hoorn (2006) and Boonstra *et al.* (2015) report foraminiferal organic linings and calcareous tests as well as mangrove pollen (*Zonocostites*) in some of the above-mentioned localities. In Tres Islas, Los Chorros and Buenos Aires, linings and tests of *Ammonia*, *Elphidium* and *Trochammina* were found (6 to 49 individuals in 1 cm<sup>3</sup> sediment for linings and 10 to 30 g sediment for tests). Other localities reached counts of 300 tests,

which is the case of Nuevo Horizonte in Peru (number 24 in Fig. 6.1). The organic linings despite lacking definitive systematic identification seem to be produced by the same genera of calcareous tests (Boonstra *et al.* 2015). Some of these calcareous tests (15% of the assemblage) were reported to have abnormalities in shape like extra, protruding chambers, with distorted arrangements and reduced size. The ecology of these organisms point to euryhaline conditions (wide range of salinity toleration) and show they are common in shallow marine environments like ponds, lagoons and mangroves, with such occurrences for instance in the Caribbean (Javaux and Scott 2003, Molinares *et al.* 2012). Their morphological aberration is a response to stressful environmental conditions like salinity, oxygen and organic matter (Boltovskoy 1991, Geslin *et al.* 2000). They represent phenotypic responses to environmental stress. In sum, evidence from foraminifera is in agreement with dinocyst ecology, pointing to shallow marine, productive coastal areas like estuaries or mangroves.

(2) *Contamana* (site 3 in Fig. 6.1)

The Pebas sediments have been recently described in detail for the Contamana area in Peru (Antoine *et al.* 2016). Two palynological samples of middle Miocene and middle-Late Miocene age yielded rare (~1%) dinocysts belonging to the genera *Brigantedinium*, *Trinovantedinium* (three indeterminate species), *Impletosphaeridium*, *Cleistosphaeridium*, *Lingulodinium*, *Spiniferites* and another unidentified dinocyst. These are the same genera present in the Mariñame/Apaporis/Iquitos area and in core 105-AM. Although without specific identifications, a similar ecological requirement can be inferred. In addition to dinocysts, foraminifera (dominant *Ammonia*), sea urchins, ostracods (mainly *Cyprideis*) and a wealth of ichthyofauna and mammals is also recorded. The fossiliferous content and sedimentology of this section in Contamana is interpreted as representing coastal plains with

marginal marine influence to estuarine embayments. This parallels the situation interpreted for other areas including core 105-AM.

(3) *Llanos basin (site 2 in Fig. 6.1)*

A newly analysed borehole documented the environmental history of the Llanos basin in Colombia during the late early Miocene to the latest late Miocene (Jaramillo *et al.* in prep). The rich palynological assemblages coupled with numerical age estimates derived from graphic correlation (see Chapter 4) allows a quantitative comparison of environments in the Llanos to those recorded here in the Solimões/Pebas system in western Amazonia (Fig. 6.6). The specific composition of dinocysts from Saltarin is fairly similar to that of core 105-AM, with dominant taxa being the Protoperidinioids (indeterminate RBCs), *Q.?* *condita* and *Spiniferites*. Moreover, *O. israelianum*, *L. machaerophorum*, *P. zoharyi*, *T. vancampoe* and many species of *Tuberculodinium* are present. The ecological requirement of this assemblage is the same discussed for the western Amazonia sites. For instance, *O. israelianum*, *T. vancampoe* and *P. zoharyi* constrain the environment to low latitude shallow waters (Zonneveld *et al.* 2013). Species of the genera *Erymnodinium*, *Selenopemphix*, *Sumatradinium* and *Trinovantedinium* together with the Protoperidinioids attest to a highly productive environment to sustain high numbers of nonphotosynthetic or heterotrophic dinoflagellates (Fensome *et al.* 1993). The abundance of such taxa is especially indicative given that protoperidiniacean cysts are sensitive to post-depositional degradation through oxidation (Hopkins and McCarthy 2002, Zonneveld *et al.* 2007, 2010), which points to two non-mutually exclusive scenarios: (1) blooms of these taxa and consequently high amounts of cysts reaching depositional environments, and (2) a high and stratified water table leading to anoxic or semi-anoxic conditions and therefore cyst preservation. Furthermore, large numbers of heterotrophic cysts in shelfal environments can be related to enhanced nutrient levels through fluvial/deltaic inputs (Dale 1996, Biffi and Grignani 1983, Duffield and Stein 1986).

Considerable spikes of foraminiferal linings were also recovered from the Saltarin core samples (up to 94% of the total sum, whereas dinocysts ranged from ~1% to >50%). Unfortunately they were not identified to any taxonomic level, but their presence in high numbers attests to the pronounced marine influence in the area. Overall, the Saltarin locality corroborates and gives better age constraints to the long known marine advances into northwest South America from the Caribbean sea (Lorente 1986, Rull 2001, Bayona *et al.* 2007), including the Llanos basin that is in a proximal position to the sea and eventually connected it to the western Amazonia region.

The comparison between Saltarin and 1-AS-105-AM shows a good correspondence of events (Fig. 6.6). Both marine incursions detected in 105-AM (MF1 and MF2) are paralleled with similar spikes in marine elements in the Llanos. Differences are also evident. The marine influence at the Llanos is clearly stronger as its episodes lasted longer and supported a richer dinocyst fauna (30 taxa vs. 21 in 105-AM), not to mention remarkably more foraminiferal linings. Two freshwater/brackish events in western Amazonia (FW2 and FW3) coincide with marine peaks in the Llanos. During these phases, freshwater algae were abundant in western Amazonia. The freshwater phases were interpreted as lakes and megalakes. *Pediastrum* is a good indicator of low energy freshwater environments (Weiler 1985), but some of its species can also not only survive but thrive in low salinities (Batten and Grenfell 1996, Head *et al.* 2005). This environmental plasticity could reinforce the brackish nature of the lakes that developed in western Amazonia synchronously with marine peaks in the Llanos. Why more frequent or longer episodes of marine influx did not occur in western Amazonia requires an explanation. Factors hampering the full transgression of the stronger and long-lasting marine phases from Llanos into western Amazonia could be related to (1) local tectonic controls, (2) fluvial migrations increasing the freshwater input into lakes, and (3) higher precipitation, also strengthening the freshwater input. Such mechanisms have

been proposed on the basis of molluscan strontium, oxygen and carbon isotope studies that reconciled low estimated salinities in Pebas deposits (~1 psu or less) with abundant Andean and cratonic freshwater runoff (Vonhof *et al.* 2003). Local uplifts controlling the impact and geographical extension of marine incursions are hard to prove. Not enough detailed reconstructions exist, and the ones available point to late Miocene activity, like those in the Iquitos forebulge area (Roddaz *et al.* 2005, and see Chapter 4) and the Vaupés range (Mora *et al.* 2010), which may represented the northern boundary of the western Amazonas basin and therefore the ‘portal’ into the Llanos basin (Mora *et al.* 2010).

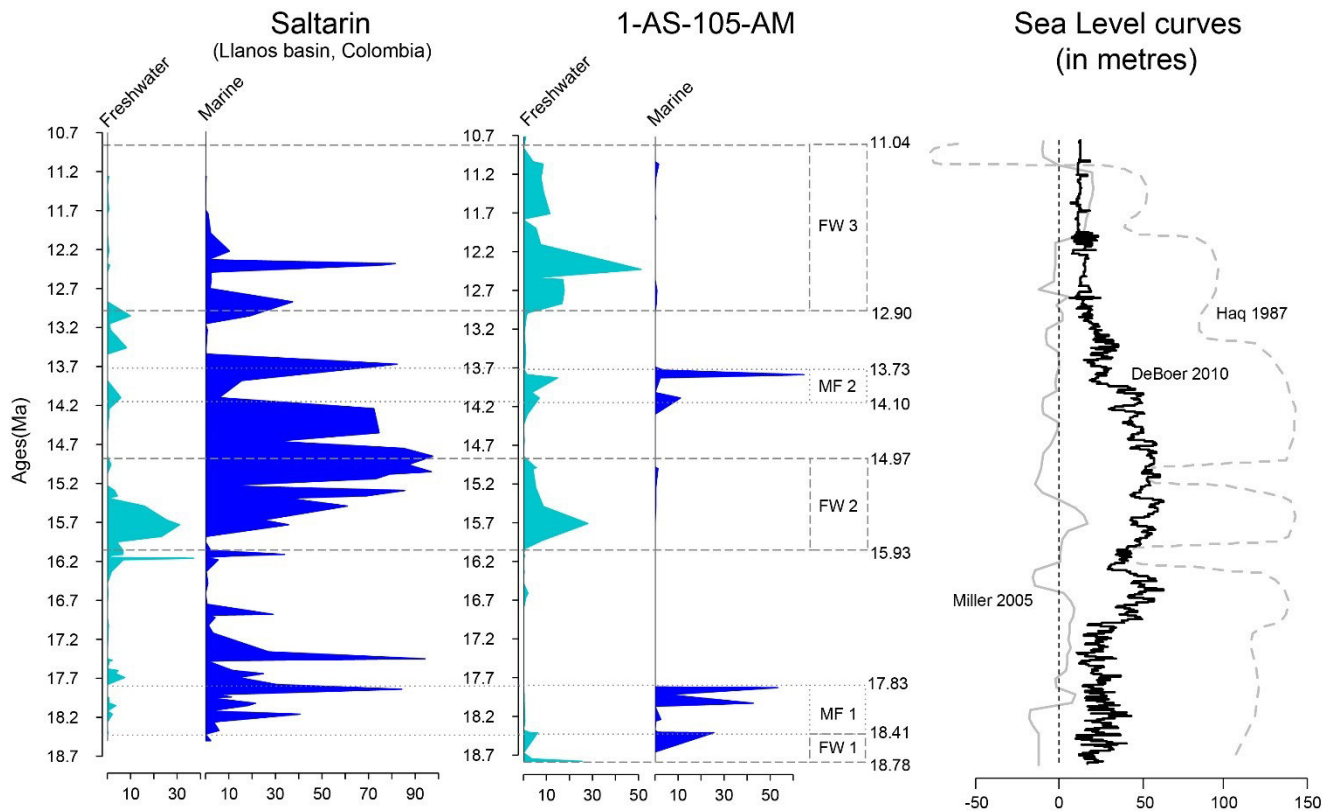


Figure 6.6. Comparison of proxies for freshwater (*Pediastrum* and *Botryococcy*s) and marine influence (dinocysts, acritarchs and foram linings) between cores Saltarin in the Colombian Llanos and 1-AS-105-AM in western Solimões Fm. Percentages are in relation to total count (all palynophs included). Sea level estimates from the same period from Haq (1987), Miller *et al.* (2005) and De Boer *et al.* (2010). Sea level curve by Müller *et al.* (2008) was not plotted for clarity, it is a nearly flat line ca. 60 m a.s.l. Zones (MF and FW) are bracketed the same way in both cores for comparison purposes.

### *Geographical extension and frequency of inundations*

Boonstra *et al.* (2015) and Antoine *et al.* (2016) recognised three incursion phases in the Pebas deposits: (1) in the early Miocene, (2) in the late early and middle Miocene and (3) in the late Middle to early late Miocene. Their early Miocene inundation can be correlated with MF1 of the present study. Their late early to middle Miocene can be correlated with either MF1, FW2 or MF2 - discrepancies are due to outcrops being short and thus ages cannot be well constrained. Most likely, it is the middle Miocene incursion (MF2) that correlates with middle Miocene sites of Boonstra *et al.* (2015), based on locality Nuevo Horizonte that demonstrates notable spikes of foraminiferal tests. This is the only marine proxy comparable to the dinocyst abundance of MF2. The late middle to early late Miocene inundation is correlated with the brackish conditions found in FW3. A further marine phase during the late Miocene was also suggested by Uba *et al.* (2009), this is outside the scope of the present study. In short, both peak marine phases and the upper brackish conditions of FW3 seem to have regional correlates, pointing to at least three phases of widespread marine/brackish conditions in western Amazonia.

Regarding the total extension of the marine incursions, there is evidence for both events as far south as the Contamana region in Peru ( $\sim 7^{\circ}1'S$ , Fig. 6.1) (Boonstra *et al.* 2015, Antoine *et al.* 2016). For the middle Miocene event (MF2) the evidence suggests as far south as the Fitzcarrald region also in Peru ( $\sim 10^{\circ}3'S$ , Fig. 6.1) (Salas-Gismondi *et al.* 2006, Antoine *et al.* 2007, Bianucci *et al.* 2013, Boonstra *et al.* 2015). Altogether, these extensions account for approximately 1,900 and 2,200 km, respectively, from the Caribbean Sea. The Fitzcarrald arch only uplifted during the Pliocene (Mora *et al.* 2010), in contrast with other late Miocene uplifts (e.g. Iquitos arch, Roddaz *et al.* 2005), so older sediments are probably still buried in the Fitzcarrald area and that explains the lack of early Miocene marine fossils in this area. Moreover, very likely a further marine incursion during the late Miocene reached

as far south as Bolivia (Uba *et al.* 2009). In this case, there should be no physical barrier for either of the marine incursions allowing constraint of their geographical extension during the Miocene. Hence the north-south axis was of the same proportions in all events.

#### *Eastern limit of the marine reach?*

Core 105-AM is the easternmost locality where evidence exists for marine incursions in the Pebas system. Maps of the geographical extension of the marine reaches tend not to overpass this area (e.g. Boonstra *et al.* 2015). Two arguments can be used to support this observation. First, the overall morphology of the Solimões/Pebas deposits exhibits decreasing thicknesses eastward (Chapter 4, Fig. 4.6, Maia *et al.* 1977, Silva-Caminha *et al.* 2010, Latrubesse *et al.* 2010). In Northern Peru (Wesselingh *et al.* 2006b) and Acre region (Maia *et al.* 1977), boreholes reached over a thousand metres whereas in the eastern and north-eastern parts of the Pebas system, boreholes reached the basement with less than 200 metres (Hoorn 1993). This configuration represents a migrating depocentre, which is typical of foreland basin systems like western Amazonia (DeCelles and Gilles 1996), and in this case is an east-migrating depocentre. Therefore, with deeper areas westward, it is plausible to assume that full marine incursions would reach preferentially the deeper areas and marginally the eastern parts. The second argument is that two middle-late Miocene cores studied by Silva-Caminha *et al.* (2010) in the Solimões Formation did not contain any marine elements. Cores 1-AS-19-Am and 1-AS-27-AM are 100 to 220 km, respectively, east of the 105-AM core (Fig. 5.6). Sampling effort or methodological differences related to laboratory processing of palynological samples could explain the lack of marine elements in these cores, otherwise they provide good evidence of the geographical limits of the marine incursions.



### *Effect of tectonics and sea level change*

Western Amazonian basins evolved in direct response to Andean uplift. The Andes have uplifted since the late Cretaceous (Martin-Gombojav and Winkler 2008, Roddaz *et al.* 2010, Hoorn *et al.* 2010), but mountain building peaked in the Neogene. The exhumation history of north and central Andes has been revealed by Apatite Fission Track analysis (Hoorn *et al.* 2010) and it shows three main uplift waves: at the Oligocene-Miocene boundary (~23 Ma), at the late Miocene (~12 Ma), and during the Pliocene (~4.5 Ma). During uplift, accommodation space was created in the forelands, which resulted in pronounced subsidence during the Neogene, including the Pebas wetland system. Vast areas of western Amazonia have altitudes of up to 120 m. For example, all 84 CPRM/Petrobrás cores (Figs. 1.2 and 5.6) were drilled in localities ranging from 70 to 120 m over an area of ~13,000 km<sup>2</sup>. The record presented here (~18.7 to 10.7 Ma) lies between the two first peaks in uplift (~23 to 12 Ma) and notably it goes across the second and strongest of them at ~12 Ma. This accelerated uplift during the late middle and late Miocene led to higher elevations in the Andes (~2,000 m a.s.l.) and as a result rainfall increased in the eastern flank causing abundant water and sediment supply to the sedimentary foreland basins (Uba *et al.* 2007, Poulsen *et al.* 2010, Hoorn 1993).

Concomitant with the tectonic and sedimentary history in western Amazonia, sea level was also fluctuating. Estimates of sea level evolution are contentious. Some estimates show high uncertainty when using global ocean basin dynamics for proxies (e.g. Müller *et al.* 2008). Others rely on sedimentary records (Haq *et al.* 1987, Miller *et al.* 2005), while other authors apply mathematical models linking sea level to ice volume and temperature derived from oxygen isotopes (De Boer *et al.* 2010) to explain sea level fluctuations. The majority of estimates agree that during the period studied here sea level was higher than present (Fig. 6.6 and references therein). Assuming the rather low gradient topography from western

Amazonia to the oceans and higher than present sea level, it is evident marine incursions could reach the studied sites without great difficulties. A precise comparison is not possible to make because of sea level estimate discrepancies and also due to the lack of an error estimation in the age model used for cores 105-AM and Saltarin. Nevertheless, it is interesting to see that basically the entire record of the wetlands including marine incursions takes place during high sea stands, that the most pronounced sea level rises happen during the late early and early-middle Middle Miocene and this parallels the longest and strongest marine incursion in the Llanos basin, eventually reaching western Amazonia (Fig. 6.6). Although still high, late middle and early late Miocene sea levels dropped, but at this time a peak in uplift renews foreland sedimentary dynamics that can explain the marine incursion in the Llanos and the paralleled freshwater/brackish megalake interpreted for western Amazonia (FW3; Fig. 6.6).

### *Vegetation*

The terrestrial palynomorph assemblage clearly shows humid tropical conditions throughout the entire studied period (Fig. 6.2). The dominance by pollen of grasses, aquatics, palms and other trees (Fig. 6.2, Fig. 6.5) is indicative of floodplains, marshes and surrounding *terra firme* forests. The suite of aquatics, palms, grasses and sedges can be interpreted as swamps and marshes (also known as *chavascal*), this is especially the case of abundant palm species *Mauritiidites* (= *Mauritia*/*Mauritiella*) that tend to form palm swamps (*buritizal*). Grasses, sedges and aquatic plants are also typical of *chavascal* (Junk and Piedade 1997). The combination of abundant grasses with *Ranunculacidites* (= *Alchornea*) is typical of primary succession communities establishing in sand bars and overbanks of *várzeas* (Wittmann *et al.* 2010). These are replaced by secondary or later succession communities represented by some palms, *Bombacacidites* spp (Bombax trees), and other trees like *Retitrescolpites? irregularis*

(=*Amanoa*), whose most widely distributed species is typical of *várzea* and riparian forests (Secco *et al.* 2014), *Ilexpollenites* (= *Ilex*) that can be found in late succession *várzeas* (Wittman *et al.* 2010) and *Ladakhipollenites? caribbiensis* (= *Sapium*) from both late succession *várzeas* and *terra firme*. Palms combined with other trees also point to *terra firme* forests. The high abundance of ferns can be derived from both floodplains and *terra firme* communities where they tend to be rather abundant in the understory, slopes and near streams (Hopkins 2005, Costa *et al.* 2005, Zuquim *et al.* 2008). In general, pollen is sourced from the nearby flooded systems like *várzeas*, marshes and palm swamps. Besides, the many woody taxa point to contribution from non-flooded forests (*terra firme*) as well. A high number of pollen taxa with unknown affinities (ca. 68% of the pollen species, or 17% of the pollen sum) was composed of tricolporate, reticulate or other ornamentations - such morphologies are more common among woody groups than herbs (Bush *et al.* 2004), so the proportion of trees should be higher than was estimated. A common aspect of tree communities in Amazonia is a strong skewed abundance distribution (ter Steege *et al.* 2013), with a very high proportion of low abundance and rare taxa. This is seen in the pollen spectra under study.

The range of forms that were linked to an extant botanical group (Appendix table 9.2) gives confidence to the vegetation reconstruction attempted. Affinities established in most cases are genus-specific (e.g. *Mauritia*, *Alchornea*, *Sapium*, *Crematosperma*, *Aspidosperma*, *Geissospermum*, *Macoubea*, *Ilex*, *Shcefflera*, *Euterpe*, *Korthalsia*, *Humiria*, *Bombax*, *Catostema*, *Ceiba*, *Pachira*, among many others). Family-level affinities like Arecaceae, Poaceae, Melastomataceae, Cyperaceae, Moraceae, and others, when in association with each other or specific ecological groups (e.g. aquatics) do not leave much room for uncertainty regarding their parental biomes. Therefore, in spite of not complete, the botanical affinity list procuded is confidently robust for paleoenvironmental interpretations.

Poaceae pollen attained high abundances (Fig. 6.5), and is essentially represented by one species, *Monoporopollenites annulatus*, which is a family-level morphology. Although Poaceae can be dominant in open vegetation types like savannahs (e.g. central Brazilian cerrados, Salgado-Laboriau 1979), there are reasons to believe the pollen spectra here identified has no affinity with dry environments. First, the lack of a diverse herbaceous community is evidence that no other biome was installed in the area - Poaceae has a bipolar palynological signal and its use as openness (and aridity) indicator is questionable (Bush 2002) and only indicated when associated with other herb groups (Absy *et al.* 2014). When not indicating aridity, Poaceae pollen in high abundances is an evidence of marshy vegetation, primary succession or floating meadows that are rather common in Amazonian rivers nowadays and other Neotropical lakes and wetlands (Absy 1979, Bush 2002, Gosling *et al.* 2009). This interpretation agrees with the overall picture of vast wetlands covering western Amazonia in the early and middle Miocene. Higher Poaceae counts were observed towards the top of section 105-AM (Fig. 6.5), this can be explained by thicker and more frequent sand deposits (Fig. 2.1) that document fluvial channels that in turn produce bars and create room for the establishment of pioneer and early successional vegetation, that has a dominant grass cover.

Overall, the entire pollen sequence here analysed shows a continued presence of tropical humid-warm conditions. Pollen taxa indicative of open or dry-wooded habitats (like wooded savannahs) were not identified. Although without thorough analytical approaches, other pollen records in the region are in agreement with the data presented presently as they do not show any evidence for floristic changes during the Miocene (Hoorn 1993, 1994a, 1994b, Silva-Caminha *et al.* 2010). A detailed floristic comparison should be performed in order to assess geographical homogeneity of plant associations across inundations. This,

however, will require a much better taxonomic consistency amongst palynologists, who should aim to unify taxa and thus increase among-site comparability.

Presence of mangrove is well defined by spikes of the pollen *Zonocostites ramonae* (= *Rhizophora*). Hoorn (2006) found a dominance of this species in three sections in the Apaporis river area (25 to 85% of the pollen sum) near Mariñame (Fig. 6.1). Other localities with comparable spikes of *Zonocostites* are Tres Islas and Santa Isabel, also in the Mariñame area. Other occurrences of this taxon are given by Hoorn (1994a, 1994b) but with lower amounts (~10% or less in Mariñame, Pijuayal and Los Chorros, and rare in Iquitos, Santa Teresa, Mocagua and core 4a-AM). An early Miocene age can be safely given to Mariñame, Tres Islas, Santa Isabel and core 4a-AM. A late early to middle Miocene stage is proposed to all other localities (see age correlations in Chapter 5). In core 105-AM the only spike of *Zonocostites* is in the early Miocene (MF1) at ~18.4 Ma, what would be in agreement with abundance spikes in early Miocene sequences at Mariñame, Tres Islas and Santa Isabel. In the middle Miocene there are rare to moderate abundances of mangrove pollen in this area, with no spike having been recorded. Given the abundance pattern discussed above, it can be inferred that large areas of mangrove developed during the early Miocene in the region of southern Colombian, western Brazilian and northeast Peruvian Amazonia, but probably spread for a much larger geographical area. Mangrove during the middle Miocene is also suggested but less clear, it is probable that mangrove occurred in other areas of western Amazonia and *Zonocostites* pollen reached the depositional sites mentioned above through water or wind transportation instead of being locally present. This would explain low abundances to rare occurrences where otherwise the taxon attains remarkable spikes.

A striking result found here is that nearly no variation in the vegetation can be explained by the flooding phases whether they are brackish or marine (CCA, Table 6.1). A methodological bias regarding the over-dominance of one environment over the others cannot

account for this result as half of the duration (3.94 Ma or 49.25%) of the studied record is non-inundated. Some imprecision in this interpretation could still exist given that the geographical extent and depth of each freshwater inundation are very hard to estimate. It still is remarkable that marine phases did not affect the vegetation structure at all, except of course by leading to short phases of mangroves. This resilience of the forest can be explained by the marginal character of the studied section. As discussed above, the westernmost part of the Solimões Formation was less affected by the inundations than other parts of the Pebas system. In a landscape context, this translates into a higher proximity of broad areas of *terra firme* forest to the Pebas systems. These *terra firme* forests were installed in central and eastern parts of the Solimões basin, in drainage areas whose rivers ran westwards into the Pebas system. If locally extirpated, forests could regain their composition and structure from the surrounding species pool that was readily available to recolonize drying inundated areas. A stabilising trend of plant communities has been seen in glacial-interglacial cycles in higher latitudes (Clark and McLachlan 2003, Blarquez *et al.* 2014), somewhat comparable to the western Amazonia inundation dynamics. In both, ecosystem divergence does not seem to exist with passing time but stabilisation, thus reinforcing the suggestion of a resilient forest that expands back to its original extent in a short temporal scale (few millennia) when either temperature or habitat/ecosystem is propitious. This idea can also be supported by ecotonal areas bordering Amazonia, where forest re-expanded with ameliorating climatic conditions of the Holocene (Absy *et al.* 1991, Mayle *et al.* 2000). The results found are not surprising given the marginal nature of core 105-AM - a detailed pollen record in a more central part of the Pebas system would be desired to more carefully address the question of whether plant communities are affected by inundations or not.

## 6.4. Conclusions

The palynomorph assemblage retrieved from core 1-AS-105-AM (18.7 to 10.7 Ma) in western Amazonia revealed vast extensions of wetland, megalakes and marine incursions coming from the Caribbean. This period is referred to as the Pebas system and evolved in response to Andean tectonics and had impacts from sea level fluctuations. Two pronounced marine phases were identified based on dinocyst spikes at 18.4 - 17.8 and 14.1 - 13.7 Ma, they were relatively rapid (0.58 to 0.37 Ma, respectively) and did not affect forest structure and composition, at least not in the marginal areas of the Pebas system. All evidence from dinocyst ecology points to assemblages adapted to shallow waters, coastal areas like estuaries and mangroves in an overall equatorial setting. Indeed, mangroves developed in the early Miocene (~18.4 Ma) and probably during the middle Miocene, as evidenced by *Rhizophora* pollen. The intervening landscape was composed of marshes, floodplains, *terra firme* forests and freshwater lakes with eventual brackish conditions. The brackish conditions are interpreted from dinocysts that point to connection of large areas and therefore megalake conditions. The Pebas system extended from southwestern Amazonia to the Llanos Basin in Colombia where marine incursions were longer and stronger during the same studied period.

## Chapter 7: Plant diversity across the Mid Miocene Climatic Optimum in western Amazonia

### 7.1. Introduction

The origin of the highly diversified Neotropical forests is a topic hotly debated in the literature. Megathermal, angiosperm-dominated biomes may have existed since the mid Cretaceous ~100 Ma in South America (Davis *et al.* 2005), but it is from the late Paleocene (~58 Ma) of north-western South America that fossils assigned to modern plant groups give us the best picture as to when the Neotropical forest structure and diversity first developed (Wing *et al.* 2009). A modern composition of the forest at the family level has remained relatively stable since the early Paleogene (Ricklefs and Renner 2012), which means tropical forests have existed for at least 60 Ma. Throughout this time, the Neotropics have acted as a cradle for species, where speciation and extinction happen rapidly (Antonelli *et al.* 2015). To the best of our knowledge, these originations and extinctions appear not to be random, but positively correlated with temperature (Jaramillo *et al.* 2006, 2010b). That has been the case at least from the Paleocene to early Miocene. Plant diversity as measured by pollen data shows bursts of in diversification during warm phases and, conversely, reductions in species diversity during cooling periods like the onset of Oligocene glaciations ~34 Ma ago (Jaramillo *et al.* 2006). This relationship of temperature and diversification has been used to empirically demonstrate an underlying driver of speciation in tropical forests (i.e. temperature) and to show that these forests have undergone considerable warming without collapse of the ecosystem.

This seemingly direct link between climate and diversity has not, however, been demonstrated for the Neogene period (23-2.5 Ma). Pollen data from the Llanos of Colombia (Hoorn *et al.* 2010) and from western Amazonia (Jaramillo *et al.* 2010a) reveal no apparent



changes of diversity that can be related to climate. An exception might be the recently published pollen record in Panama, where there is an increase in richness from early to late Miocene (Jaramillo *et al.* 2014). Unfortunately a temporal gap covering part of the early and mid-Miocene as well as taphonomic issues related to lithofacies prevent a more detailed picture of when the diversity increase happened. Regardless of change or stability in the Neogene records mentioned above, a more comprehensive study of plant diversity during this period of time is completely lacking in northern South America, including the Amazon forest.

The objectives of this chapter are to describe the pollen diversity (here used as number of species) in core 1-AS-105-AM and to test if there are significant changes of pollen richness across the Mid Miocene Climatic Optimum (MMCO, Zachos *et al.* 2001, 2008), and across the marine incursions already detected (see chapter 6). The studied section constitutes a very good model for the intended analysis since (i) it has a constant and linear accumulation in an overall homogeneous continental environment, (ii) is well sampled, and (iii) it spans the period from 18.7 to 10.7 Ma (see chapter 5) and therefore captures the time before, during and after the MMCO. The full methods applied in this chapter can be found in Chapter 3.

### ***The Miocene climate***

The Neogene world is characterised by a long term cooling punctuated by a warming phase (Zachos *et al.* 2001, 2008). Early Miocene (23-16 Ma) global temperature gradually cooled, but at ca. 17 Ma a transient warming event is superimposed on this general cooling trend and lasted until ca. 14 Ma. This 3 Ma period is known as the Mid Miocene Climatic Optimum (MMCO) and temperatures could have risen ~3 to 4 Celsius degrees compared to today (Zachos *et al.* 2001, You *et al.* 2009, Goldner *et al.* 2014). This warming is the last significant one in the planet's geological history and can be compared to modelled late 21<sup>st</sup> century scenarios (ca. 3°C by 2100, IPCC 2014), hence being a possible analogue for future

climate change, although warming rates were in the millennial-million year scale rather than decade-century scale as presently. Proceeding this warming stage, temperatures cooled down gradually in what is known as the Mid Miocene Climatic Transition (MMCT), when the whole planet got colder and glaciations intensified in the northern hemisphere. Global vegetation responded to this climatic evolution by expanding and compressing biomes in high latitudes (Pound *et al.* 2012). In western Amazonia, vegetation for the period comprised in the MMCO and MMCT is characterised by wetlands, floodplains and evergreen upland forest (*terra firme*) (Hoorn 1993, 1994a, 1994b, Silva-Caminha *et al.* 2010), with no evidences for biome changes. Many important constituents of the present day Amazon lowland plant diversity were already in place during the Miocene (Cuenca *et al.* 2008, Meerow *et al.* 2009, Dick *et al.* 2013).

## **7.2. Results**

Ninety five samples were analysed for their pollen and spores content. From those, 70 were chosen for the diversity analysis as they had pollen counts of at least 226. This ensured samples utilized had a similar size and thus biases related to sample size could be avoided (Fig. 7.1.a). A further three samples were excluded because they clearly were evenness outliers (Fig. 7.1.b), such samples have a hyperdominance by one or two taxa and as a result diversity measurements are largely biased. This procedure guaranteed a fair comparability of sample regarding diversity metrics.

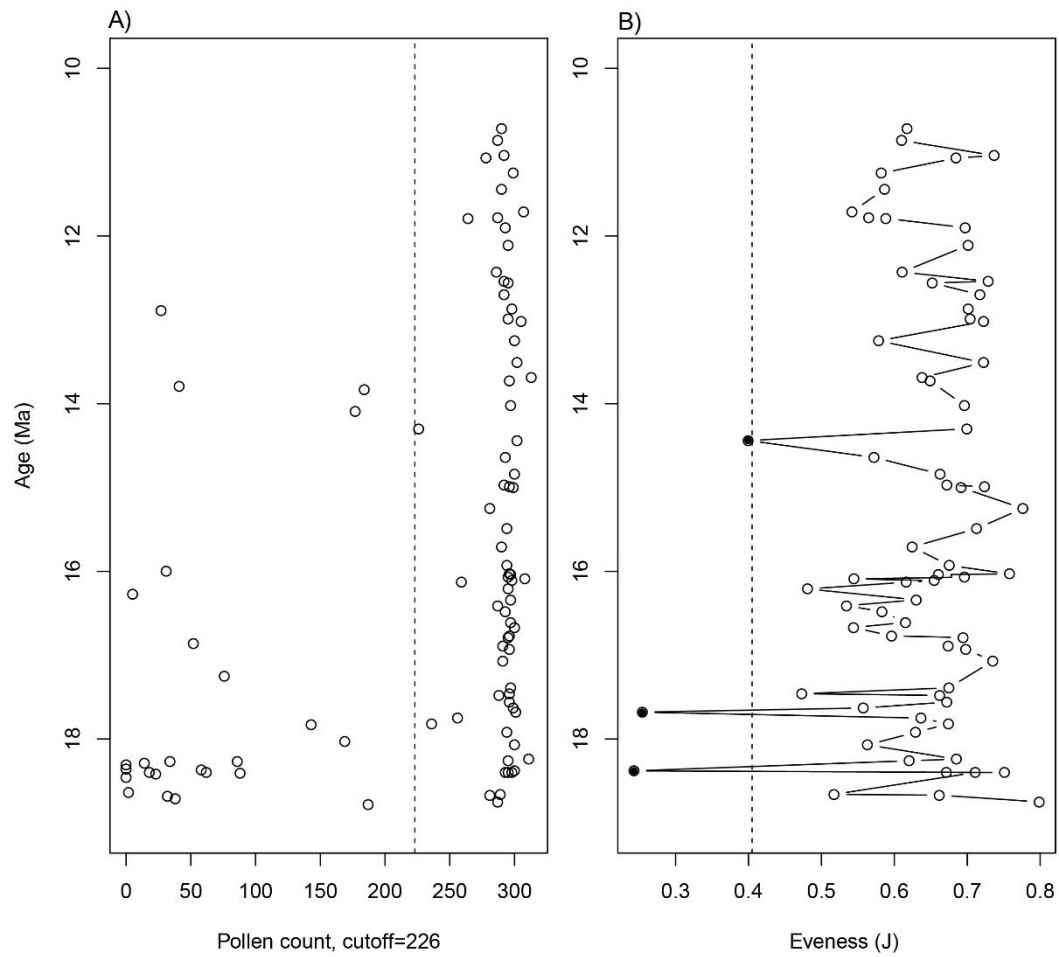


Figure 7.1. A) Pollen counts for the initial 95 samples plotted against age, dashed line is cut off of 226. B) Evenness for the 70 samples chosen for diversity analysis, dashed line is a threshold of 0.4 J below which samples were removed from data set (three solid symbols), number of remaining samples is 67.

### *Within-sample diversity and ecological ordination*

Within sample diversity metrics display an evident pattern of increasing values at ca. 16 Ma (Fig. 7.2. a and b). Rarefied diversity and H' diversity increased 46.8% and 20%, respectively. This diversity increase is accompanied by an even stronger community change at the same age as measured by the ecological ordination (Fig. 7.2. c and d). The DCA results (Table 7.1) reveal that axis one is responsible for most of the variation, totalling 40.3%. Axis two is responsible for 26.8%; however, a good part of this variation is caused by the position of the bottom three samples while the great majority of samples orbit a similar value (Fig. 7.2.c) and there is no significant variation of scores before and after 16 Ma ( $w=568$ ,  $p$ -value=0.9). Hence the exploration of variations is focused on axis one, which indeed accounts for a 70% change from pre to post 16 Ma. Across marine incursions there are no apparent changes in neither diversity nor community scores. In fact, the effect of inundations on plant composition is negligible or completely undetected (see Chapter 6).

Table 7.1. Summary results of Detrended Correspondence analysis (DCA). Percentages in bold are how much variation each axis explains.

	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.2263 ( <b>40.3%</b> )	0.1503( <b>26.8%</b> )	0.09987( <b>17.8%</b> )	0.08388 ( <b>14.9%</b> )
Decorana values	0.2309	0.1682	0.08906	0.06850
Axis lengths	2.2032	2.3556	1.30600	1.66649

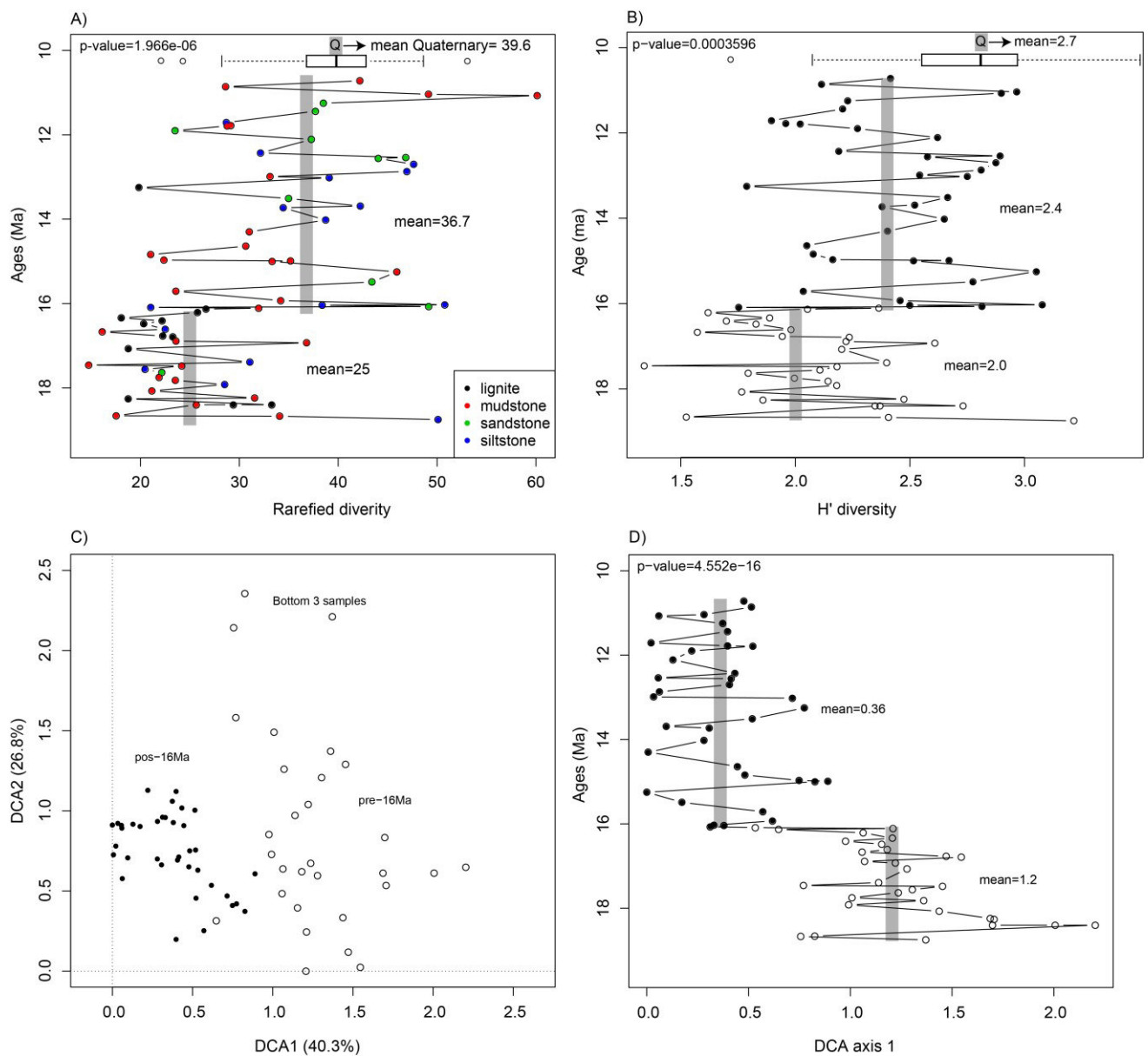


Figure 7.2. A) Rarefied diversity, lithology of samples is colour coded. B) Shannon ( $H'$ ) diversity. C) Detrended correspondence analysis (DCA, Table 7.1) plot of axis 1 and 2, open symbols are samples older than 16 Ma, solid symbols are samples younger than 16 Ma. D) DCA axis 1 scores plotted against time. For all plots: grey bars are mean values for groups pre and post 16 Ma, p-values refer to Mann-Whitney U tests.

### *Potentially taphonomic biases*

An analysis of variance was performed in order to test the effects of strata (age) and lithology on the diversity and ecological metrics. The ANOVA results (Table 7.2) reiterate the significant differences of all diversity and ecological metrics when older (strata >16 Ma) and younger (strata <16 Ma) ages are compared. The ANOVA also shows no significant differences in evenness, thus confirming abundances distributions of taxa are not affecting diversity estimates differentially. What is more, there is a clear effect of lithology on all metrics, but no interaction between lithology and strata was found (Table 7.2). A closer inspection on what generates these significant differences of lithology on the analysed metrics was carried out with a Tukey test (results are summarised in Appendix Table 9.3.4), and the main driver of such results is lignite. Samples of lignite have lower diversities and higher DCA axis one scores than other lithologies (Fig. 7.3). This could be caused by a real underlying vegetation signal, as sediments are capturing the very local vegetation signal, i.e. the immediate surroundings only rather than a larger catchment area - since lignites are formed from peats that accumulate in bogs, marshes and swamps and therefore they tend to be representative of local plant communities (Traverse 2007, Jardine and Harrington 2008). Another issue with the lignites in the present study is that they are concentrated on the lower part of the section and are not distributed evenly in time. Similarly, sands are concentrated in the upper part of the section (Fig. 7.2.a). These distinctions in lithology distribution over the core can be problematic and bias the results as depositional systems may differ and not be evenly represented throughout the core. In order to tackle this, the complete analysis was re-run firstly excluding lignites, and secondly excluding both lignites and sands. This way, a more isotaphonomic subset of the data could reveal if the pattern of diversity increase and community change at 16 Ma is real or a product of taphonomy. The results of these analyses can be seen in Fig. 7.4, they show that all significant differences are maintained when lignites

and sands are removed from the data set. Also, invariably the bottommost sample is a high diversity outlier for the pre-16 Ma stage, and when excluded from the data the differences are even more significant (Fig. 7.4). Furthermore, when siltstones and sandstones are combined (38.8% of the data set) and analysed, they also retain the previous patterns: for rarefied (W=112, p=0.006914) and H' diversity (W=105, p=0.02547), and for DCA axis 1 (W=1, p <0.0001). When only mudstones are analysed (43% of the total data set) the pre and post 16 Ma groups are significant with regard to rarefied within-sample diversity (W=157, p=0.0196) and DCA axis 1 (W=143, p=8.841e-07) but not H' diversity (0.09161).

Table 7.2. Summary results of analysis of variance to test the effect of lithology and strata (age) on diversity, evenness and DCA axis 1 scores. Lithologies tested were lignite, mudstone, siltstone and sandstone; Strata tested were older (pre-16Ma) and younger (post-16Ma). For the Shapiro-Wilk normality test, p-values > 0.05 mean that the null hypothesis (that the data are normally distributed) cannot be rejected, thus the normality assumption was met for the ANOVA.

		Df	Sum sq	Mean sq	F value	Pr(>F)	Shapiro-Wilk
Rarefied diversity	Lithology	3	12.61	4.203	7.739	<b>0.000192***</b>	
	Strata	1	7.43	7.431	13.685	<b>0.000477***</b>	<sup>1</sup> W=0.97246
	Lithology:strata	3	1.77	0.591	1.089	0.360957	p=0.1429
	Residuals	59	32.04	0.543			
H' diversity	Lithology	3	1.757	0.5856	4.147	<b>0.00983**</b>	
	Strata	1	0.930	0.9301	6.586	<b>0.01283*</b>	W=0.99312
	Lithology:strata	3	0.271	0.0903	0.639	0.59280	p=0.9738
	Residuals	59	8.332	0.1412			
Evenness	Lithology	3	0.01339	0.004462	0.882	0.448	
	Strata	1	0.00831	0.008311	1.643	0.205	W=0.97861
	Lithology:strata	3	0.00714	0.002379	0.470	0.704	p=0.3017
	Residuals	59	0.29842	0.005058			
DCA axis 1	Lithology	3	1.9034	0.6345	13.005	<b>1.26e-06***</b>	
	Strata	1	3.0204	3.0204	61.909	<b>9.14e-11***</b>	<sup>1</sup> W=0.97648
	Lithology:strata	3	0.0924	0.0308	0.631	0.598	p=0.2341
	Residuals	59	2.8784	0.0488			

Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

<sup>1</sup>square-rooted

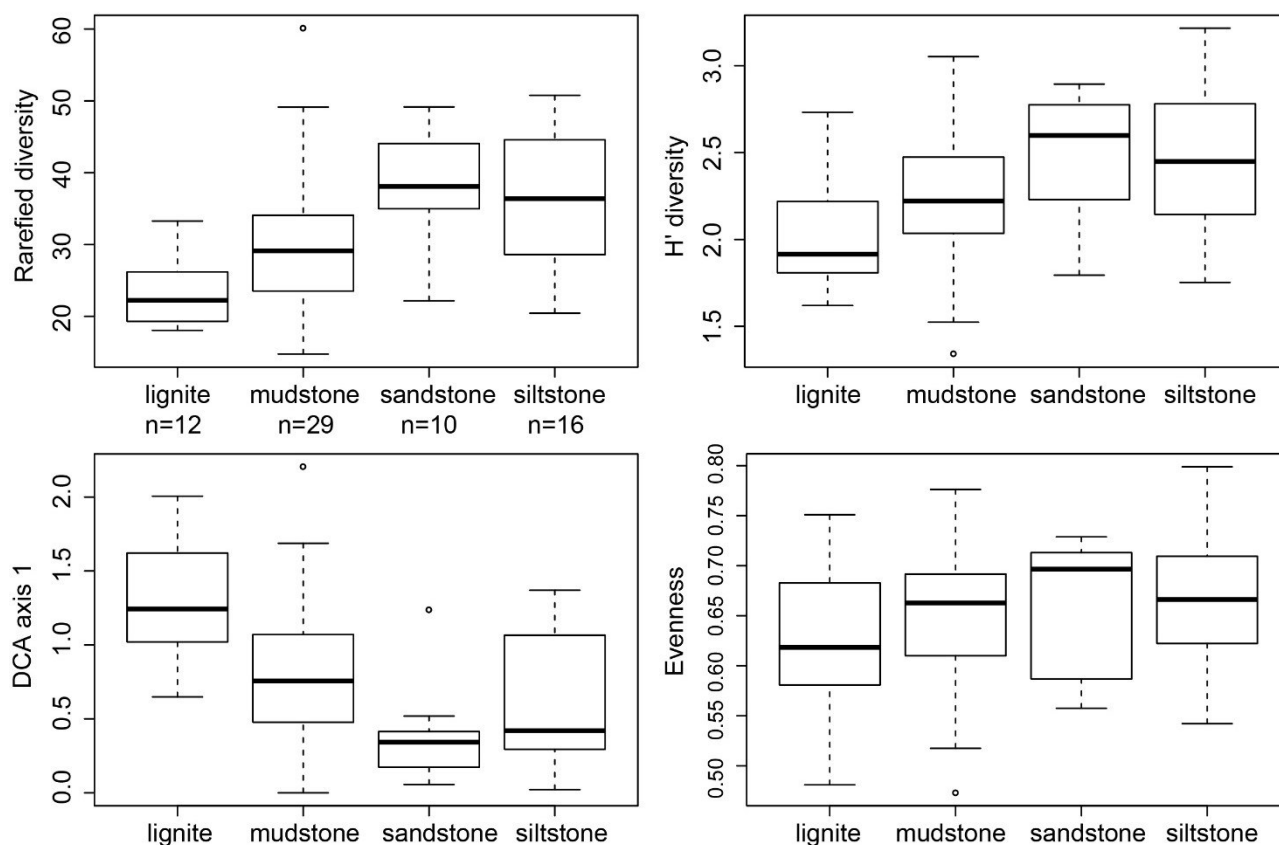


Figure 7.3. Boxplots of diversity metrics, DCA axis 1 scores and evenness for each individual lithology (details of ANOVA in Table 7.2).

### *Among-sample diversity*

Among sample estimates agree with the overall results of the within sample estimates, although with some discrepancies. The following comparisons are at a sample pool of 31 as this is the total number of samples of the smaller group (pre-16Ma). The expected species richness for the rarefaction curves increased 18.3%, from 229 before 16 Ma to 271 after 16 Ma (Fig. 7.5.a). Chao2 estimator increased 14%, from 442 to 504 (Fig. 7.5.b) and Jackknife2 increased 11.4%, from 420 to 468 (Fig. 7.5.c). Except rarefied curves, Chao2 and Jackknife2 display confidence bands that overlap between older and younger groups, implying there is no significant difference of the expected number of species at a comparable sample pool (Fig. 7.5). A remarkable result seen in these estimates is the overall number of species for each



technique used. Because there are many rare taxa in the studied samples and because Chao2 and Jackknife2 estimators weigh singletons and doubletons differentially from common taxa, the total expected richness given by these estimators is greater (ca. twofold) than that given by rarefaction. When the total expected richness is compared between each group, Chao2 yielded 442 and 575 and Jackknife2 yielded 420 and 507 species pre and post 16 Ma, respectively. These results compared are significantly different (Chao2:  $W=685$ ,  $p=0.007633$ ; Jackknife2:  $W=638$ ,  $p=0.04577$ ). Taking all the above together, there is a weaker evidence, but nevertheless detectable, for higher taxonomic diversity between samples of the younger group (post 16 Ma) than of the older group (pre 16 Ma) than the evidence from these group's within sample estimates.

### *Standing diversity*

The piecewise regression performed with LAD and FAD data resulted in ages of 18.24 Ma for FAD and 11.25 for LAD (Fig. 7.6.a). This means that there is a considerable edge effect for originations older than 18.24 Ma and for extinctions younger than 11.25 Ma. Standing diversity, origination and extinction rates are then limited to the interval between these ages. The standing diversity curve (Fig. 7.6.b) has a “D” shape, i.e. increasing at the bottom and decreasing at the top, this is an indication that an edge effect is still present. Taking this into account, it is still noticeable that the maximum standing diversity is reached at 13.7 Ma with 169 taxa. This is explained by consistently higher originations than extinctions up to ca. 13.9 Ma (Fig. 7.6.c).

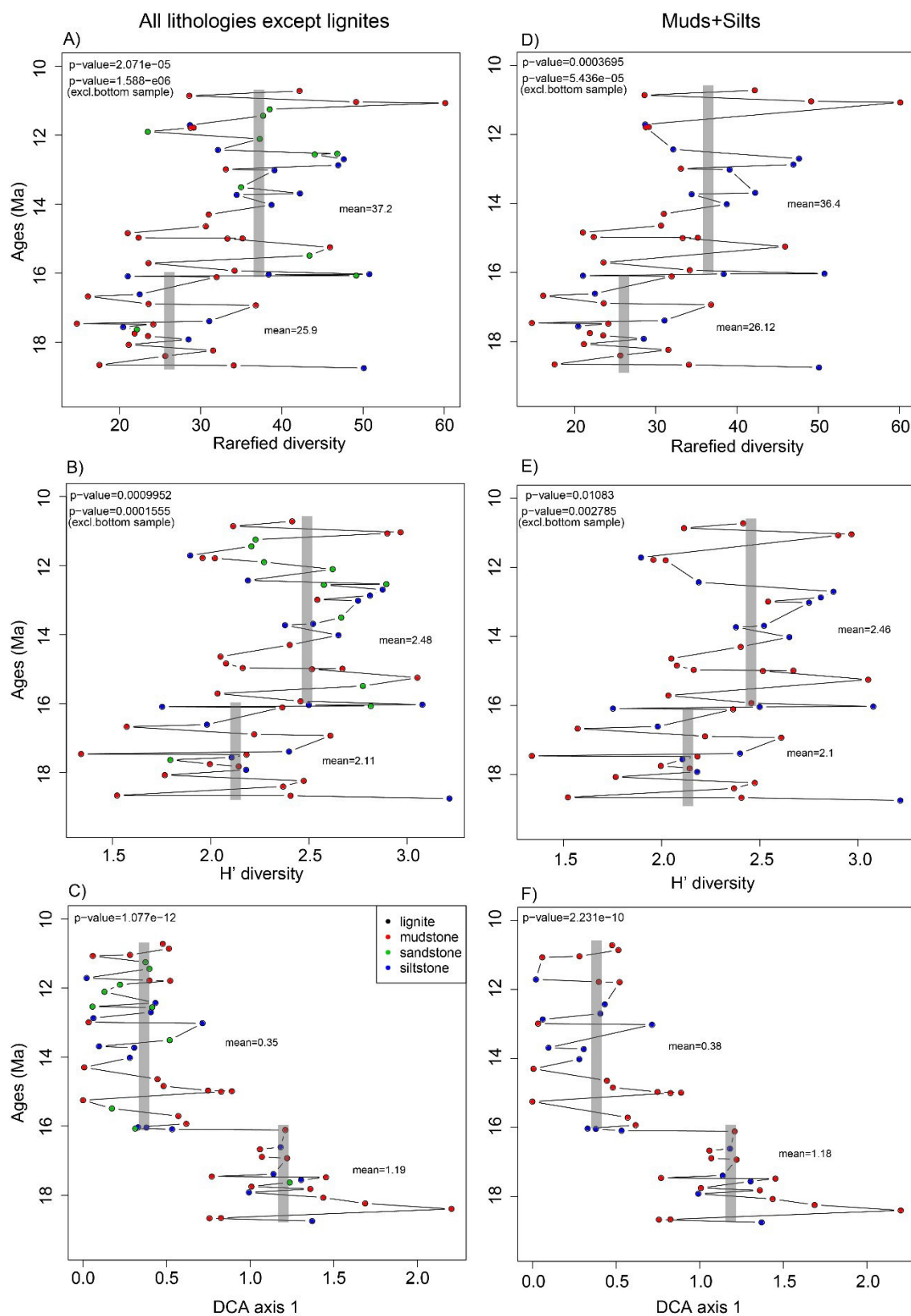


Figure 7.4. Plots of rarefied diversity (A), H' diversity (B) and DCA axis 1 (C) for data set excluding lignites, and for data set formed of muds and silts only (D, E and F). For all plots: grey bars are mean values for groups pre and post 16 Ma, p-values refer to Mann-Whitney U tests.

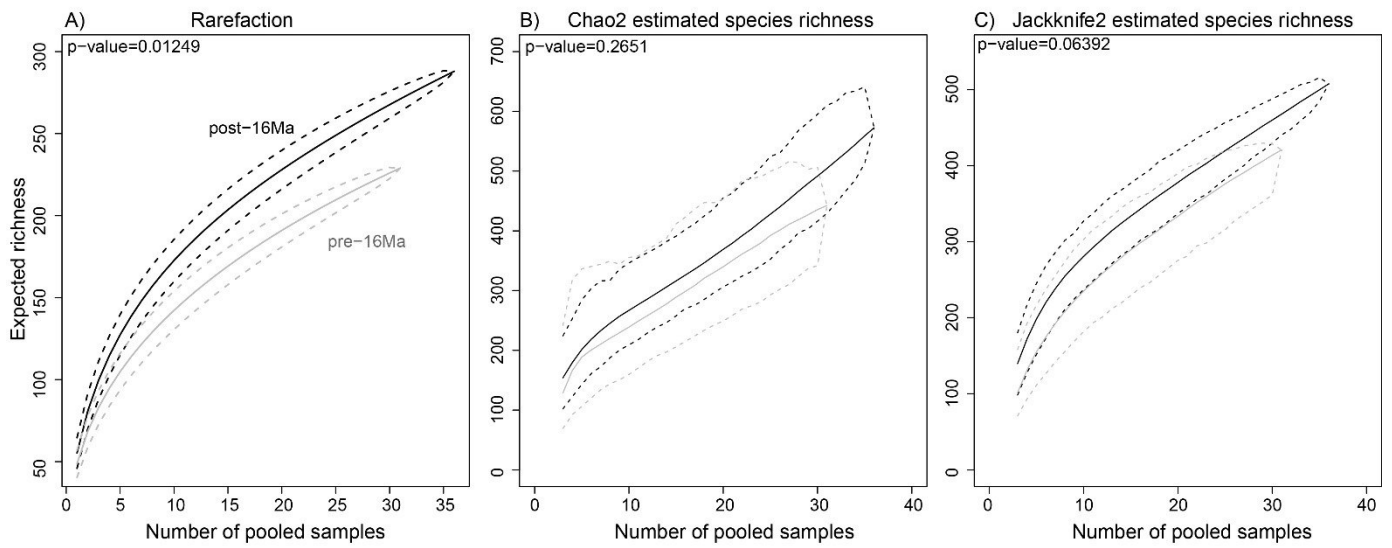


Figure 7.5. Among sample diversity estimates using rarefaction (A) and richness estimators Chao2 (B) and Jackknife2 (C). p-values refer to Mann-Whitney U tests run at a sample pool of 31 samples.

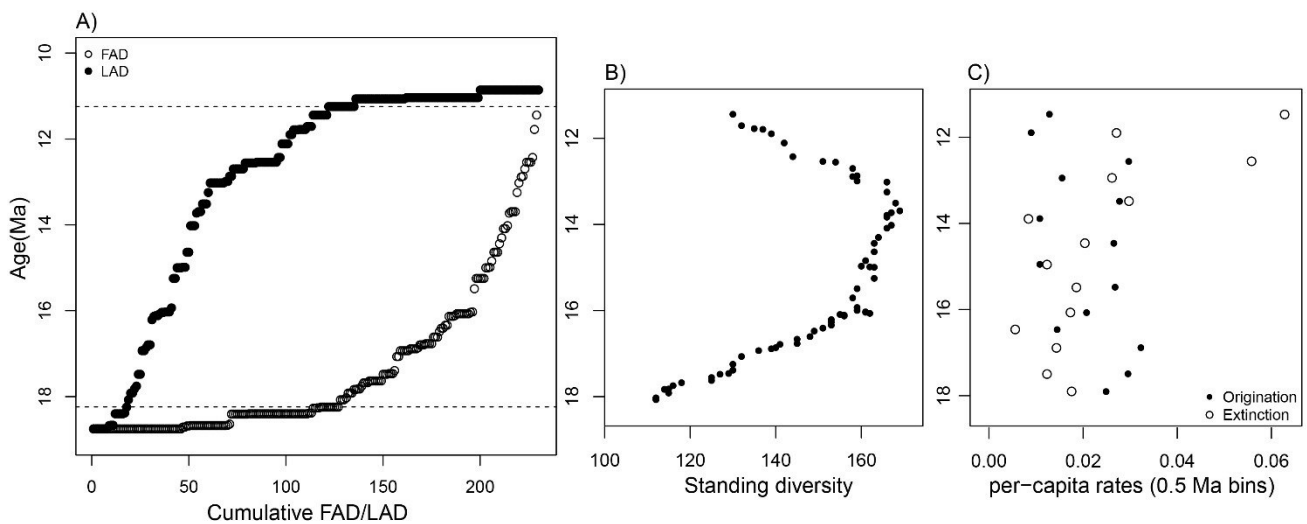


Figure 7.6. A) Cumulative FAD and LAD data plotted against time. Dashed lines are the breakpoints from the piecewise regression used to estimate the edge effect for FAD (18.24 Ma) and LAD (11.25 Ma). B) Standing diversity calculated after range-through assumption of taxa. C) Per-capita rates of origination and extinction in 0.5 Ma bins.

### Evolutionary models

Data was binned at every 0.5 Ma and time series analysis run. Unbiased random walk (URW) models fitted the data best. For rarefied diversity, URW is the best model when the full data set is used and also when lignite is excluded (Table 7.3), but in the latter case stasis is a non-negligible model (A.W. of 0.301). When only muds and silts samples are used the rarefied diversity data is fitted best for URW and stasis with similar weights. This is also the case for all data sets used for model fits of H' diversity, although for the full data set there is a non-negligible generalised random walk (GRW) model fit (A.W. of 0.242). These results reflect a nearly complete lack of directionality for diversity over time, but it is clear there is considerable variation. The picture gets more evident for models fitting DCA axis 1 scores, where regardless of the data set used GRW greatly outperforms other models. This indicates a strong directionality of the plant community. All in all, composition changes more significantly than did richness (compare model fits for diversity x DCA in Table 7.3). The evolutionary models are partially confirming the results from the diversity and ecological metrics, but with the main difference that a trajectory in diversity dynamics is not clear and the reason for this is probably a higher variation of the data post 16 Ma than pre 16 Ma.

Table 7.3. Summary of model fits to diversity and ordination metrics for pollen data. K: number of model parameters; AICc: corrected Akaike Information Criterion; A.W.: Akaike Weight; GRW: Generalised random walk; URW: Unbiased random walk. Best fits in bold, non-negligible in italic.

Data	Model	K	<u>Rarefied diversity</u>		<u>H' diversity</u>		<u>DCA axis 1</u>	
			AICc	A.W.	AICc	A.W.	AICc	A.W.
Full data	GRW	3	112.2393	0.174	8.337407	<i>0.242</i>	7.106912	<b>0.866</b>
	URW	2	109.4623	<b>0.699</b>	7.441643	<b>0.379</b>	10.848010	0.133
	Stasis	2	112.8731	0.127	7.441643	<b>0.379</b>	25.046422	0.000
Excl. lignites	GRW	3	114.6744	0.135	10.481275	0.196	6.799147	<b>0.848</b>
	URW	2	111.8078	<b>0.565</b>	9.045207	<b>0.402</b>	10.237425	0.152
	Stasis	2	113.0683	<i>0.301</i>	9.045207	<b>0.402</b>	22.630638	0.000
Muds + Silts	GRW	3	102.58017	0.098	11.050310	0.152	7.938299	<b>0.848</b>
	URW	2	99.49092	<b>0.460</b>	9.000112	<b>0.424</b>	11.389083	0.151
	Stasis	2	99.57422	<b>0.442</b>	9.000112	<b>0.424</b>	20.840422	0.001

### *Comparison between Miocene and extant diversity*

The four Lateglacial-Holocene cores yielded 75 samples above the cut-off count of 226 grains. Evenness was comparable to Miocene samples (mean  $J=0.71$  and minimum  $J=0.5$ ), therefore further sample removals were unnecessary. A total number of 237 taxa was found. Mean rarefied diversity was 39.6 (22.3 to 53.2) and  $H'$  diversity was 2.7 (1.7 to 3.5). These numbers are higher than middle Miocene values (rarefied:  $W=1057$ ,  $p=0.041$ ;  $H'$ :  $W=705$ ,  $p < 0.0001$ ) and much higher than early Miocene ones (rarefied:  $W=138$ ,  $p < 0.0001$ ;  $H'$ :  $W=214$ ,  $p < 0.0001$ ) (Fig. 7.2).

### **7.3. Discussion**

The pollen flora of western Amazonia studied here revealed a pattern of richness increase at 16 Ma. Although with high variation (Fig. 7.2a and b), diversity of the post-16 Ma period has a consistent increase of ca. 39 to 46% in the rarefied within-sample diversity, and of ca. 18% in the among-sample diversity (and of ca. 11 to 14% when using Chao2 and Jackknife3 estimators, but potentially more if errors are taken into account). Quantifying the amount of richness increase is not straightforward, but the pattern is evident. This increase in diversity is paralleled by a noticeable shift in the community data (Fig. 7.2c and d, and results of the time series analysis in Table 7.3). Together, both the diversity and community structure seem to occur in a rather sharp fashion. The overall change at ~16 Ma can be explained by a higher number of taxa being restricted to the post 16 Ma period than to the pre 16 Ma (Fig. 7.7). A total of 50 taxa only appear after 16 Ma, whereas 31 go extinct before 16 Ma. Furthermore, amongst the singletons, 92 are restricted to the post 16 Ma period, and 51 to the pre 16 Ma period. Altogether, post 16 Ma restricted taxa account for 35% of the total assemblage, a number that is similar to the within-sample rarefied diversity increase (ca. 39

to 46%). The great majority of the taxa (64%, singletons excluded), however, range through the entire or great part of the record. Another aspect that reinforces the difference between taxa before and after 16 Ma is the longer ranges of taxa after 16 Ma than pre 16 Ma. That translates into a rather discrete standing diversity of the pre 16 Ma restricted assemblage when compared to the post 16 Ma restricted assemblage (Fig. 7.7). It seems therefore that extinctions (or emigrations) are playing a minor role in causing the diversity and community change than are originations (or immigrations). In fact this can be seen in the origination/extinction per capita rates, which show higher originations across the MMCO and up to ~13.9 Ma (Fig. 7.6).

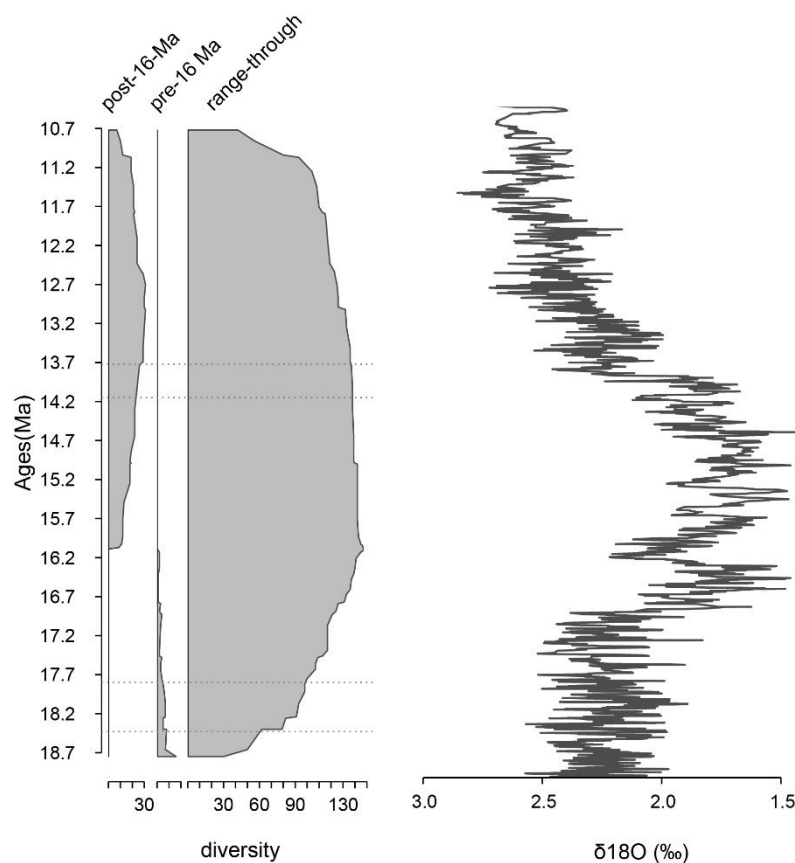


Figure 7.7. Left: Standing diversity for groups of taxa restricted to the period pre and post-16 Ma, and for those ranging-through. Right: Oxygen isotope curve of Zachos *et al.* (2001).

The observed changes in the pollen record are coincident with the beginning and duration of the MMCO (Fig. 7.7), thus suggesting a link between the climatic warming and the pollen record. Other variables do not seem to have a detectable effect on diversity and community, like for instance the inundations (see chapter 6) or taphonomic biases (see results). A statistical artefact exists regarding the edge effect (Foote 2000), however this does not affect within-sample diversity estimates or multivariate scores. Furthermore, after partially controlling for the edge effect (piecewise regression), there is still a consistent trend of higher originations than extinction which overlaps with the duration of the MMCO.

A relationship between plant communities and climate has been broadly reported for the Cenozoic of northern South America (Jaramillo *et al.* 2006, 2010b). Increases in plant diversity take place during warming periods, reminiscent of what is reported here. This relation is more robust for the Palaeogene and lower Neogene (early Miocene), but had only been suggestively shown for the remaining Miocene period, including the MMCO span (Hoorn *et al.* 2010, Jaramillo *et al.* 2014). The data reported here on diversity increase (see results) can now confirm this pattern in detail. Interestingly, the standing diversity of pollen shown by Hoorn *et al.* (2010) peaks at an age of 13 Ma, what is quite similar to the reported herein (13.7 Ma). The data used by Hoorn *et al.* (2010) comes from the Llanos region (Fig. 1.2) approximately 1,000 km from core 105-AM, hence the positive diversity response to the MMCO event is potentially synchronous in a wide geographical area. This area could be even wider if the Panama Miocene data presented by Jaramillo *et al.* (2014) is confirmed. The latter shows the similar significant diversity increase from early to late Miocene, but further studies are needed to understand when exactly this increase takes place. All these examples plus the present study agree with the idea that warmings do affect tropical forests by prompting diversification. Mechanisms underlying speciation are still obscure, they could be

related to latitudinal expansion of the tropical forests during warmer periods (Fine and Ree 2006, Fine *et al.* 2008, Morley 2000) what would lead to richer species pools due to the species-area relationship (Rosenzweig 1995) (but see Jaramillo and Cardenas 2013). Other mechanisms invoke increased metabolic rates in the tropics due to higher energy inputs and consequentially increased mutation rates (Rohde 1992, Wright *et al.* 2006). Another set of ideas contends that organisms in warm environments have accelerated biotic interactions (Dobzhansky 1950, Vermeij 2003, Schemke *et al.* 2009), which leads to stronger pressures in niche occupation and in turn to speciation. Regardless of the mechanisms driving diversification, a response by the forest to increased temperatures is clear. During the MMCO, with an estimated ~3-4°C increase (You *et al.* 2009, Goldner *et al.* 2014), Amazon forests could have experienced MAT of up to 30.5°C (assuming a present MAT of 27.5°C). This value lies within maximum tolerance of tropical plants (Krause *et al.* 2010), hence a dieback due to heat intolerance can be ruled out. Actually, molecular data for many widespread Neotropical tree species show they already existed during warmer periods, namely the late Miocene (Dick *et al.* 2013). Much stronger warmings during the Palaeogene were not able to destabilize tropical forests, they actually increased diversity (Jaramillo *et al.* 2010b). Moreover, apart from temperature a key factor defining vegetation structure is precipitation (Woodward 1987). During the Miocene in western Amazonia all evidence points to very humid conditions, including molluscan isotopic data that points to a similar seasonal monsoonal system controlled by the Inter Tropical Convergence Zone as it is presently (Kaandorp *et al.* 2005). In terms of CO<sub>2</sub>, another constraining factor for plant growth (Taiz and Zeiger 2015), estimates for the MMCO period are controversial with either similar, lower or much higher than present (e.g. Royer and Beerling 2011). Some of these estimates are two to three times present day values (for instance Kürschner *et al.* 2008, Beerling *et al.* 2009, Retallack 2009, Zhang *et al.* 2013). Increased CO<sub>2</sub> can stimulate water



use efficiency and overall plant performance (Lloyd and Farquhar 2008, Cernusak *et al.* 2011). Given that in western Amazonia water was not a limiting factor, higher temperatures and CO<sub>2</sub> can therefore be expected to promote favourable conditions for plant development. Paralleled to this favourable physiological conditions there is a dynamic system in a wide geographical area. Large-scale flooding potentially fragmented the forest that would in turn reconnect during lower water tables. This process probably varied in intensity both in time and space, so plant species had the constant opportunity of habitat re-colonisation. The combination of niche dynamics with favourable climatic-physiological conditions during the MMCO resulted in diversification of the plant communities.

A long debate has permeated evolutionary biology of tropical ecosystems – are the tropics a cradle or a museum of diversity (Stebbins 1974, Jablonski *et al.* 2006)? A current view is that the dichotomy be abandoned as evidence places the tropics in both cradle and museum scenarios (Jablonski *et al.* 2006). Antonelli *et al.* (2015) showed that for plants the Neotropics have higher rates of both originations and extinctions when compared to other tropical areas, implying that a more rapid turnover during geological time explains the higher Neotropical diversity. The data presented here agrees with this interpretation. There is a degree of correlation (~35%) between originations and extinctions (see Fig. 7.8), showing a tendency for turnover of the plant community. These dynamics cannot be fully explained by originations and extinctions as they could naturally be immigrations and emigrations in the present study due to the short interval analysed and limited geographic coverage (one borehole only). To solve that question a high number of sites, covering a broad geographical area are needed in order to understand the biogeographical histories of the species found herein. Nonetheless, it is striking that both molecular and distributional (Antonelli *et al.* 2015) and fossil pollen data from western Amazonia have a certain similarity concerning patterns of origination/extinction. The Palaeogene data of Jaramillo *et al.* (2010b) also

showed an increase in extinction in the same time bin that originations attain the highest rate (during the PETM interval), which is similar to the relationship suggested by the current data (Fig. 7.8). In both cases there is a net increase in the total pollen diversity, therefore demonstrating that although there is species replacement (turnover), the final output is a richer assemblage across warming intervals. This proposes the possibility of Neotropical forests in acting as both cradles and museums of biodiversity.

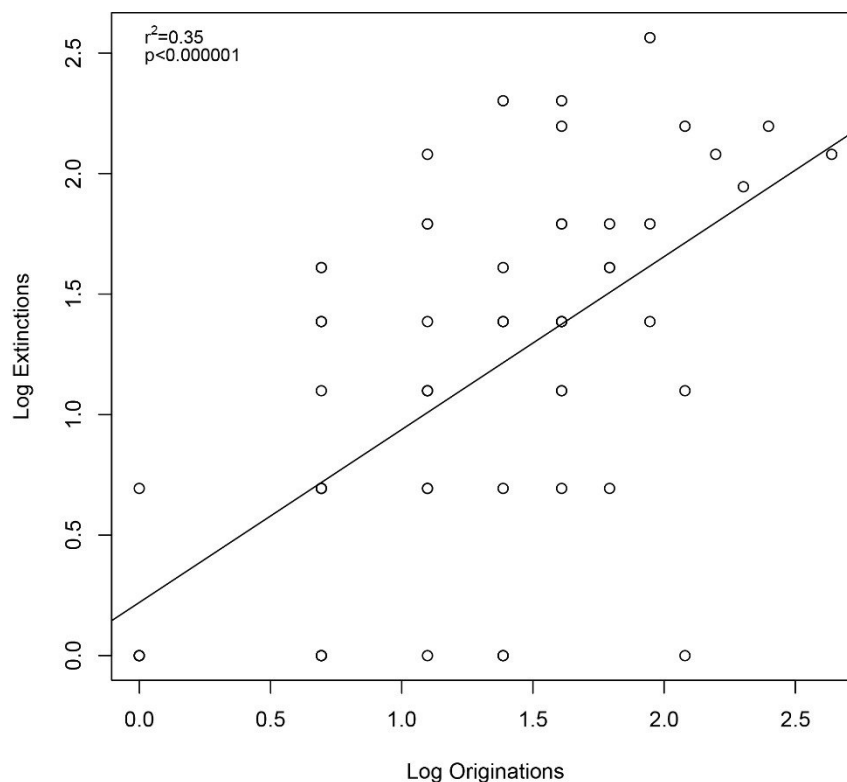


Figure 7.8. Originations and extinction display a certain degree of correlation. Data used is restricted to samples below and above the edge effect (see Fig. 7.6), singletons excluded.

Finally, the Miocene vs. extant (Holocene) comparison showed a richer pollen assemblage at the present time. The very same result had been seen by Jaramillo *et al.* (2006), who stated that diversification should have occurred from early Miocene to present in order to produce a richer extant assemblage. The authors hypothesised that it was the MMCO event that triggered such speciation. This is in full agreement with the present data and also

potentially in line with other studies (Hoorn *et al.* 2010, Jaramillo *et al.* 2014). Van der Hammen and Hooghiemstra (2000), however, claimed the contrary, that the Miocene was more species rich than the present day. They posited this after comparing Holocene with Miocene sediment samples from a similar area (Caquetá River, Hoorn 1994b) and seeing 280 pollen types in the Miocene and 140 in the Holocene. This comparison is nevertheless not possible as the time interval between samples in Holocene and older (e.g. Tertiary) sequences varies vastly (see for instance Wing 1998, Harrington and Jaramillo 2007). With a much longer interval between samples (Miocene) more species can accumulate and therefore the final species pool is richer than when only a few thousand years are comprised between samples (Holocene). A preferable comparison was done here, using the rarefied within-sample estimates that significantly showed a richer extant diversity (Fig. 7.2). Clearly, more fieldwork effort and taxonomic work must be done to improve the comparability of Miocene and extant samples. Howsoever, assuming the diversity trend depicted above it is unexpected that for the remaining period from the late middle Miocene to Pliocene the overall temperature-diversity relationship is not shown (Hoorn *et al.* 2010) as opposed to the rest of the Tertiary. Why did not diversity decrease during cooling periods from the middle Miocene Climatic Transition (MMCT) to the Quaternary (Fig. 1.1)? One possibility is that diversification outweighed extinctions when plant communities invaded the drying Pebas system. By the late Miocene, western Amazonia started to dry out as a consequence of Andean uplift (Wesselingh 2006, Figueiredo *et al.* 2009, Hoorn *et al.* 2010, Sacek 2014), and by the early Pliocene wetland areas had completely vanished (Latrubesse *et al.* 2010). With the demise of inundation, western and eastern parts of Amazonia could reconnect. Plant groups were then able to take advantage of newly formed land ecosystem and colonise or recolonise them. That is the case, for instance, of speciose families Rubiaceae (Antonelli *et al.* 2009) and Arecaceae (Roncal *et al.* 2013). These new land areas were as well uplifting

and exposing sediments very rich in cations that are nowadays reflected in consistently nutrient richer soils in western Amazonia than in eastern parts, not to mention edaphic heterogeneity (Wesselingh and Salo 2006). This difference has a direct influence in plant composition (Higgins *et al.* 2011) and translates into more diverse western forests (ter Steege *et al.* 2006, Hoorn *et al.* 2010).

## 8. CONCLUSIONS

Palynological analysis of cored sediments from western Amazonia was presented from 95 samples. The intensive taxonomic work from core 1-AS-105-AM from the Solimões Formation in NW Brazil (Chapter 2) yielded 491 different types of pollen, spores, algae, dinoflagellate cysts, acritarchs and foraminiferal linings. Remarkable is the high diversity of pollen and spores that accounted for 402 types. Of these, 76 pollen and 25 spores species were formally described as new (Chapter 4). In addition, 14 formal species from the literature were re-described in new combinations because they had originally been assigned into incorrect form-genera.

The wealth of palynomorphs in the core, meta-analysis of other palynological data from the Amazon region, and well-preserved mollusc shells in some horizons, permitted an age assignment significantly better than previous ones for the region (Objective 1.4.1). First and last appearance events of key taxa were used to perform a Graphic Correlation with a nearby pollen zonation. This zonation (Jaramillo *et al.* 2011, and unpublished results) has a calibration that allowed age assignments for individual samples via interpolation (Chapter 5). The results of this exercise were an age span from 18.7 to 10.7 Ma (late early to earliest-late Miocene) for the studied core. Furthermore, critical comparisons and reassessments of previously published pollen records from western Amazonia supported an age for the entire Solimões Formation and its lateral equivalents (Pebas Fm) of early Miocene to Pliocene. Morphology and local structural controls on the deposits of the Solimões Formation were also discussed and linked to foreland dynamics as a result of the Andean orogeny.

The combination of a more detailed age model proposed for core 105-AM when compared to previous studies (e.g. Hoorn 1993, 1994a, 1994b, Silva-Caminha *et al.* 2010) with a higher sampling resolution and excellent palynomorph recovery permitted an

improved palaeoenvironmental description for the early and middle Miocene in western Amazonia (Chapter 6, Fig. 8.1). By using presence and also relative abundance data of marine elements (dinocysts, foraminiferal linings and acritarchs) two major events of marine incursions into western Amazonia were established (Objective 1.4.2). The first occurred between 18.4 and 17.8 Ma, and the second between 14.1 and 13.7 Ma. The timing and duration for these events is the best estimate so far for the long known marine incursions in the region. Freshwater lake phases were also established in three main periods and they possibly had a minor brackish character as well.

Throughout the whole studied period, vegetation type does not change and consists of typical humid tropical forest elements. A series of statistical analyses were used to test the effect of inundation events and climate evolution on the diversity and structure of the forest (Chapters 6 and 7, Fig. 8.1). Interestingly, inundations had no detectable effect on the composition or structure of the forest as measured in the fossil pollen associations (Objective 1.4.3). This was interpreted as resilience of the forest. The exception is a short period where mangroves developed during the early Miocene. Diversity metrics, however, did show a change from lower to higher diversity at ca. 16 Ma (Objective 1.4.4). This increase occurs during the Middle Miocene Climatic Optimum, when temperature may have risen ca. 3-4° C degrees (You *et al.* 2009, Goldner *et al.* 2014), and it is concluded that this warming event drove diversification. This idea builds on previous records showing a close relationship between plant diversity and temperature in the equatorial humid forests (Jaramillo *et al.* 2006) that had not yet been properly tested for the Miocene period.

Finally, the results and discussions of the present thesis have both regional and wider implications. Regionally, the age model of core 105-AM can help improve the overall biostratigraphical framework. There is still substantial work to be undertaken, but with a more detailed age model such as the one presented here, future studies can build upon it to

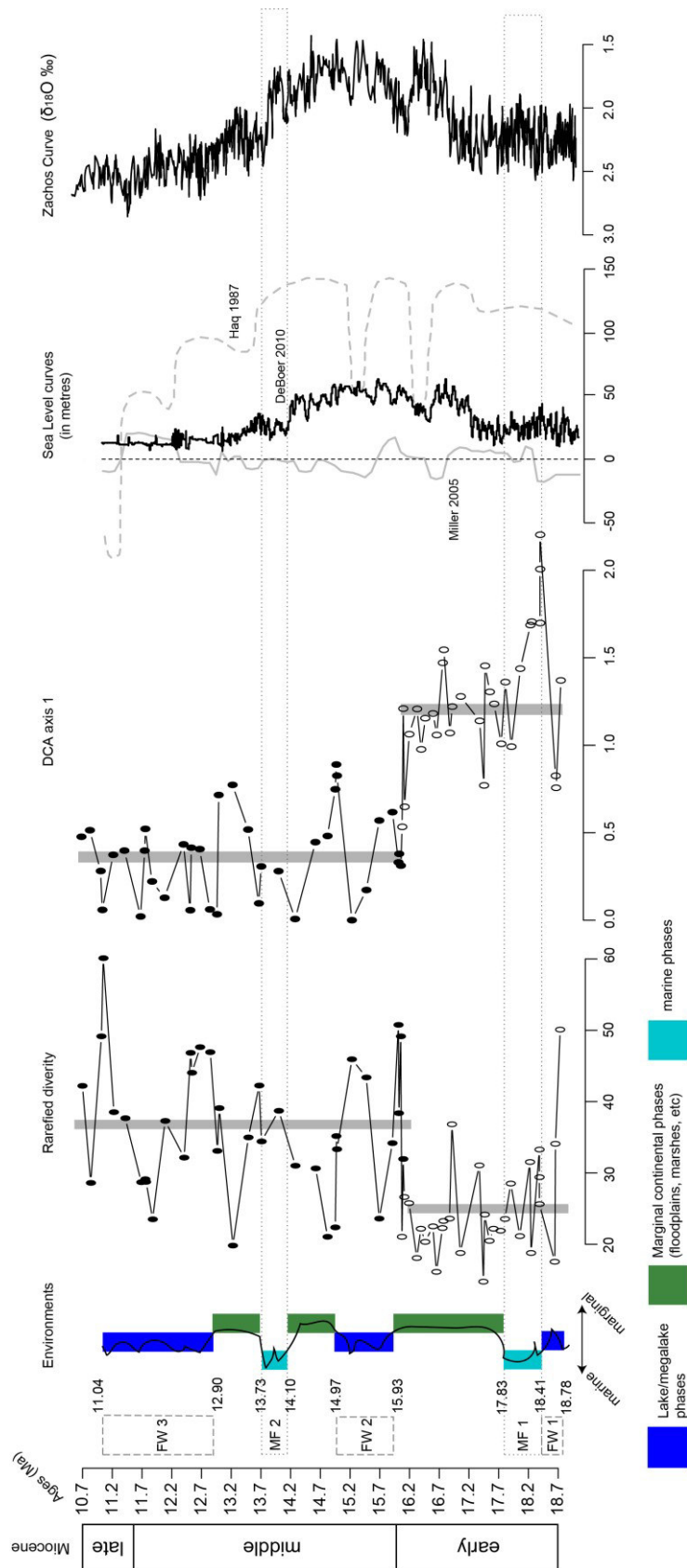


Figure 8.1. Summary schematic diagram with environments, diversity metrics from core 1-AS-105-AM, and independent global measures of sea level and temperature. Marine inundation events (MF1 and MF2) do not coincide with plant community change and diversity increase.

formulate biostratigraphical hypotheses and gradually improve the use of marker taxa in western Amazonia during the Neogene. At a broader scale, studies of diversification processes of various Amazonian organisms can more precisely incorporate the timing and duration of events described herein into their hypotheses. For instance, many aquatic groups entered and adapted to Amazonian waters from the Caribbean Sea (e.g. river dolphin, Hamilton *et al.* 2011). Do dated molecular phylogenies coincide with the inundations events? Does the appearance of certain plant and animal groups in different sites of Amazonia happen before, in-between or only after inundation events? What is the relationship between migration/speciation and the evolution of the Pebas system? These and many other questions can be asked and use the present work as paleogeographical hypotheses. Moreover, climate modellers can incorporate with more detail the lake/marine phases into climatic models of the Neogene, with potential global effects.



## 9: Appendixes

Tables 9.1. List of LAD and FAD events used in the graphic correlation (Chapter 5), Line of Correlation (LOC) equations and R functions used to derive composite units and ages.

9.1. a). Events of well 1-AS-105-AM and Composite units (CU) from the composite section of Jaramillo *et al.* (2011). FL EM= Early Miocene Flooding, FL MM = Middle Miocene Flooding; species with “ ” are informal and were added to the composite section from an initial correlation between well Saltarin and the composite section (see Appendix Table 9.1. b).

Event	CU_FAD	FAD105	CU_LAD	LAD105
Areci regio	-19960	-370.3	-1960.1	-30
Bomba araracuarensis	-9108.92	-161.7	-1471.46	-39.8
Bomba baculatus	-9777.74	-325.3	-817.278	NA
Bomba brevis	-18009.4	-324.9	-204.935	-69.8
Bomba muinaneorum	-14393.6	-370.3	-717.273	-35.4
Bomba nacimientoensi	-18335.1	NA	-2602.8	-35.4
Byttn "rugulata"	-9498.44	-110.7	-2256.62	-35.4
Camar "trilobatus"	-2630.87	-35.4	-2212.21	-35.4
Cicat baculatus	-4228.02	-130.1	-4104.23	-130.1
Cicho longispinosus	-5492.8	-165.5	-866.39	-30
Clava microclavatus	-11226.7	-324.6	-102.468	-30
Crass columbianus	-15916.2	NA	-316.93	-39.8
Crass vanraadshooven	-8823.06	-360.9	-1960.1	-34.6
Cribr sp.	-21405.9	-284	-9391.73	-284
Croto annemariae	-18077.2	-267.9	-2597.95	-110.7
Croto reticulatus	-9398.7	-359	-2323.64	-30
Cteno suigeneris	-16076.7	-359	-2163.46	-34.6
Cyclu scabrata	-18077.2	-370.3	-7393.37	-370.3
Echid barbeitoensis	-5194.03	-105.5	-4061.78	-70.5
Echin muelleri	-17465.6	-267.9	-817.278	NA
Echip akanthos	-16427.3	NA	-102.468	NA
Echip estelae	-17606.1	-370.3	-1161.15	NA
Echip intectatus	-2660.24	-272.1	-2660.24	-34.6
Echip jutaiensis	-3966.69	-230.2	-1874.4	-35.4
Echip lophatus	-4126.67	-289.9	-1874.4	NA
Echit mcneillyi	-0.6	-101.2	-573.818	-34.6
Echit spinosus	-8663.71	-324.9	-102.468	-34.6
Erici annulatus	-2522.91	-69.8	-2212.21	-35.4
FL EM	-9535.84	-293.3	-8511.18	-284
FL MM	-5342.95	-101.2	-3959.46	-96.7
Fenes spinosus	-4039.3	-75.3	-174.195	-75.3
Foveo ornatus	-15599.7	-324.9	-1474.08	-34.6
Grims magnaclavata	-9777.74	-326.2	-1874.4	NA

Heter incomptus	-10128.9	-325.3	-174.195	-34.6
Heter rotundus	-4900.76	-326.2	-0.1513	NA
Heter verrucosus	-5492	-289.9	NA	NA
Hydro minor	-5492	NA	NA	NA
Ilexp tropicalis	-9799.83	-324.9	-2212.21	-34.6
Jandu minor	-16778.9	-370.3	-3755.03	-165.5
Jandu seamrogiformis	-16808.2	-284	-1471.13	-35.4
Ladak caribbiensis	-4126.67	-187.6	-2630.87	-34.6
Laevi granulatus	-19177.8	-324.9	-727.52	NA
Lanag crassa	-17590.7	-298.9	-1975.13	-39.8
Lingu machaerophorum	-16835.3	-289.9	-3502.25	-96.7
Longa microfoveolatu	-19875.9	-110.7	-0.0402	NA
Magna grandiosus	-16032.8	-359	-174.195	-34.6
Malva maristellae	-9777.74	-250	-651.906	-34.6
Margo vanwijhei	-17708.5	-370.3	-1471.13	NA
Mauri franciscoifra	-19722.9	-370.3	-286.75	NA
Mauri franciscoimin	-18917.8	-325.3	-0.1513	NA
Mauri franciscoipac	-19482.1	-76.7	-3995.93	-69.8
Monop annulatus	-19904.9	NA	-71.7273	NA
Multi vanderhammenii	-5001.31	-267.9	-789	-30
Nijss fossulatus	-10419.3	-289.9	-758.26	-34.6
Parso brenacii	-3930.96	-298.9	-0.6	-44.7
Perfo digitatus	-17454.6	-298.9	-924.7	-34.6
Peris pokorny	-17038	NA	-0.1513	NA
Polya mariae	-4173.47	-298.9	-2522.07	-44.7
Polyp planus	-9636.79	-210.1	-1878.11	NA
Polyp pseudopsilatus	-14176.4	-155.1	-143.455	-35.4
Polyp sp.	-19913.1	-324.9	-0.0402	-34.6
Polyp specious_aff	-17818.7	-360.9	-1317.26	-34.6
Polyp usmensis	-16304.6	NA	-789.04	NA
Prote triangulatus	-14548.2	-370.3	-1878.11	-30
Proxa tertiaria	-19987.8	-370.3	-563.571	-34.6
Psila devriesii	-17963.1	NA	-1471.13	-79.9
Psila fissilis	-18346.2	-298.9	-1962.39	NA
Psila garzonii	NA	-298.9	NA	-35.4
Psila herngreenii	-9129.27	-359	-3852	-53
Psila marinamensis	-7393.37	-359	-4390.81	-35.4
Psila minimus	-16849.4	-294.5	-0.4	-120.9
Psila nanus	-16116.9	-359	-917.984	-69.8
Psila obesus	NA	-230.2	NA	NA
Psila redundantis	-16720	-325.3	-14354.3	-39.8
Psila silvaticus	-9334.42	NA	-1878.11	-30
Psila triangularis	-17815.1	-299.3	-1021.17	-79.9
Pteri gemmatus	-17815.1	-254.3	-174.195	-91.5
Quadr condita	-9432.78	-298.9	-3236.33	-52.9
Quaternary	-1415	-20	NA	NA

Ramon	-5958.74	-405	-5733.06	-330
Ranun operculatus	-16685	-370.3	-0.4	NA
Retib retibolus	-19961.8	-210.1	-1975.13	NA
Retib yavarensis	-15549.9	-182	-1960.1	-161.7
Retim absyae	-5437.47	-283.2	-3221.87	-30
Retis crassiannulatu	-16711	-325.3	-1474.08	-75.3
Retit caputoi	-16116.9	-326.2	-1947.27	-79.9
Retit crassicostatus	-4647.01	-125.3	-4647.01	-44.7
Retit irregularis	-17816.1	-370.3	-0.1047	NA
Retit kaarsii	-14637.3	-359	-1894.29	-39.8
Retit lorentae	NA	-272.1	-1330.73	NA
Retit magnus	-17963.1	-53	-15604	-53
Retit simplex	-18066.4	-370.3	-543.078	-140.9
Retit traversei	-7393.37	-44.7	-2335.18	-44.7
Rhoip guianensis	-18066.4	NA	-1317.26	NA
Rugut arcus	-9432.78	-30	-2212.21	-30
Rugut felix	-17038	-325.1	-0.4	-91.5
Silta dilcheri	-16116.9	-267.9	-3223.84	-39.8
Solimoes	-5733.06	-330	-1415	-20
Spiro spiralis	-18077.2	-250	-1471.13	-44.7
Stria anastomosatus	-3742.15	-324.9	-3223.84	-34.6
Stria catatumbus	-17817.3	-165.5	-789.04	NA
Stria poloreticulatu	-9777.74	-364.8	-0.1513	NA
Stria saccolomoides	-16169.7	-155.1	-563.571	-35.4
Tuber vancampoae	-9411.42	-293.3	-1894.29	-96.7
Verru etayoi	-16114.7	-324.3	-2490.5	-51.6
Verru rotundiporus	-14964	-26.35	-1317.26	NA
Zonoc ramonae	-17372.7	-370.3	-817.278	-34.6

9.1. b). Events of well Saltarin and Composite units (CU) from the composite section of Jaramillo *et al.* (2011). FL EM= Early Miocene Flooding, FL MM = Middle Miocene Flooding; species with “ ” are informal. Leon and Guayabo are Formations in the Llanos basin.

<b>Taxa</b>	<b>FAD_CU</b>	<b>FAD_Salt</b>	<b>LAD_CU</b>	<b>LAD_Salt</b>
Bomba araracuarensis	-9108.92	-518.94	-1471.46	-144.15
Bomba baculatus	-9783.12	-659.93	-817.278	-396.22
Bomba baumfalki	NA	-657.3	-3812	-575.38
Bomba brevis	-18009.4	NA	-204.935	-167.65
Bomba muinaneorum	-14393.6	-662.33	-717.273	-372.38
Bomba nacimientoensi	-18335.1	-396.22	-2777.9	-167.35
Brevi microechinatus	-18314.3	-612.76	-15024.1	-372.38
Bytn "rugulata"	-4540.11	-644.25	-3721.8	-99.53
C1	-9026.57	-608.2	-5453.74	-546.9
C2	-9728.67	-654.6	-9026.57	-608.2

C3	-10506.2	-671	-9728.67	-654.6
Camar "trilobatus"	-3721.8	-172.85	-3721.8	-90.83
Cicho longispinosus	-5492	-550.43	-866.39	-90.83
Clava densiclavatus	-19906.5	-628.61	-10548.9	-406.95
Clava microclavatus	-11226.7	-622.78	-102.468	-90.83
Corsi psilatus	-19944.5	-548.24	-0.1513	-145.35
Corsi undulatus	-17604	-636.8	-0.0402	-99.53
Crass columbianus	-15916.2	-659.93	-316.93	-169.77
Crass vanraadshooven	-10056.7	-622.78	-1960.1	-172.85
Crico guianensis	-19893.8	-638.33	-15878.6	-145.35
Crico macroporus	-17708.5	-622.78	-12096.5	-622.78
Croto annemariae	-18077.2	-657.3	-4093.51	-166.4
Croto reticulatus	-10042.1	-640.65	-3683.21	-112.66
Cyath annulatus	-2661.24	-178.8	-81.974	-90.83
Cyclu scabrata	-18077.2	-641.88	-7393.37	-612.76
Echim gracilis	-16849.4	-178.8	-16068	-167.65
Echim solitarius	-17496.1	-386.52	-16450	-112.66
Echin muelleri	-17465.6	-644.25	-817.278	-90.83
Echip akanthos	-16427.3	NA	-102.468	-112.66
Echip estelae	-17606.1	-523.9	-1161.15	-203.77
Echip lophatus	-9303.38	-430.82	-1874.4	-409.52
Echit "microechinatu	NA	-520.35	NA	-143.07
Echit acanthotrileto	-14764.6	-641.88	-4385.34	-97.29
Echit spinosus	-9780.04	-523.9	-102.468	-90.83
Echit trianguliformiorb	-17598	-372.38	-16068	-372.38
Echit variabilis	-17603.8	-543.38	-15750.4	-90.83
Erici annulatus	-4000.24	-151.7	-3721.8	-90.83
FL EM	-9411.42	-645.6	-9215.71	-619.75
FL MM	-4388.72	-547.18	-4298.46	-408.56
Fenes spinosus	-4039.3	-422.69	-174.195	-99.53
Foveo ornatus	-15599.7	-417.55	-1474.08	-90.83
Grims magnaclavata	-9790.03	-659.93	-1874.4	-99.53
Guayabo	NA	-441.8	NA	NA
Heter incomptus	-10128.9	-550.43	-174.195	-114.92
Heter rotundus	-9790.03	-529.95	-0.1513	-86.3
Horni lunarensis	-18498.1	-638.33	-10294	-622.78
Ilexp tropicalis	-9780.04	-662.33	-3716.09	-90.83
Jandu minor	-16778.9	-662.33	-4399.63	-372.38
Jandu seamrogiformis	-16808.2	-657.3	-1471.13	-101.35
Ladak caribbiensis	-6063.63	-430.82	-3591.72	-172.85
Laevi granulatus	-19177.8	-548.24	-727.52	-143.07
Lanag crassa	-17590.7	-657.3	-1975.13	-97.29
Leon	-5453.74	-546.9	-3893.7	-441.8
Lingu machaerophorum	-16835.3	-413.49	-3502.25	-413.49
Longa microfoveolatu	-19875.9	-657.3	-0.0402	-278.37
Lumin colombianensis	-16755.3	-543.38	-16194	-144.15

Magna grandiosus	-16032.8	-659.93	-174.195	-99.53
Malva maristellae	-9091.86	-659.93	-651.906	-97.29
Malva spinulosa	-15785.1	-657.3	-4408	-99.53
Margo vanwijhei	-17708.5	-622.78	-1471.13	-184.33
Mauri franciscoifra	-19722.9	NA	-286.75	NA
Mauri franciscoimin	-18917.8	-662.33	-0.1513	-144.15
Monop annulatus	-19904.9	-659.93	-71.7273	-90.83
Multi vanderhammenii	-9011.84	-539.77	-789	-90.83
Nijss fossulatus	-10419.3	-537.29	-758.26	-143.07
Pachy diderixi	-3115.55	-654.97	-3047.95	-654.97
Palae cingulatus	-3905.37	-435.01	-1945.49	-90.83
Parso brenacii	-9621	-167.65	-0.6	-144.15
Perfo digitatus	-17454.6	NA	-924.7	-145.35
Perin reticuloacicul	-19979.5	-586.7	-102.468	-145.35
Peris pokorny	-17038	NA	-0.1513	-97.29
Polor absolutus	-18441.7	-101.35	-16102.8	-101.35
Polya mariae	-9621	-166.4	-2522.07	-166.4
Polyp echinatus	-18586	-539.77	-17563.8	-539.77
Polyp planus	-7004.07	-650.29	-1878.11	-376.26
Polyp sp.	-19913.1	-657.3	-0.0402	-90.83
Polyp usmensis	-16304.6	-662.33	-789.04	-112.66
Polys subtile	-16867.7	-510.03	-817.278	-510.03
Prote dehaani	-20458.8	-586.7	-19732.2	-174.98
Prote triangulatus	-14548.2	-586.7	-1878.11	-99.53
Proxa operculatus	-19976.7	-619.75	-817.278	-396.22
Pseud perfectus	-17538.9	-650.29	-15999.2	-650.29
Psila devriesii	-17963.1	-575.38	-1471.13	-97.29
Psila fissilis	-18346.2	-659.93	-1962.39	-433.27
Psila herngreenii	-10042.1	-626.73	-3852	-626.73
Psila marinamensis	-10042.1	-612.76	-3721.8	-455.4
Psila minimus	-16849.4	-144.15	-0.4	-99.53
Psila nanus	-16116.9	-627.36	-917.984	-474.6
Psila pachydermatus	-15521.1	-662.33	-0.0402	-586.7
Psila robustus	NA	-629.9	-14424.2	-86.3
Psila silvaticus	-3898.56	-638.33	-1878.11	-203.77
Psila tesseroporus	-4363.15	-659.93	-2045.22	-659.93
Psila triangularis	-17815.1	-614.35	-1021.17	-101.35
Psila venezuelanus	-16105	-662.33	-4114.9	-99.53
Pteri gemmatus	-17815.1	-520.35	-174.195	-178.8
Quadr condita	-9621	-641.88	-3236.33	-408.56
Ranun operculatus	-16685	-657.3	-0.4	-90.83
Retib retibolus	-19961.8	-638.33	-1975.13	-372.38
Retib triangulatus	-17589	-184.33	-15794	-184.33
Retib yavarensis	-15549.9	-90.83	-1960.1	-90.83
Retim absyae	-9205.58	-549.23	-3683.21	-278.02
Retip crotonicolumel	-4352.09	-510.03	-866.39	-97.29

Retis angeli	-18863.5	-657.3	-16120.8	-396.22
Retis crassiannulatu	-16711	-641.88	-1474.08	-150.63
Retis festivus	-17608.2	-654.97	-16002.9	-654.97
Retit baculatus	-18586	-638.33	-15896.5	-442.42
Retit caputoi	-16116.9	-662.33	-1947.27	-167.35
Retit irregularis	-17816.1	NA	-0.1047	-90.83
Retit kaarsii	-14637.3	-622.47	-1894.29	-167.65
Retit simplex	-18066.4	-659.93	-543.078	NA
Retit sommeri	-15729.8	-548.24	-604.558	-151.7
Retit traversei	-3966.69	-612.76	-3227.58	-114.92
Retit wijningae	-3355.76	-638.33	-3355.76	-638.33
Rhoip guianensis	-18066.4	NA	-1317.26	-90.83
Rhoip hispidus	-18041.9	-659.93	-1471.46	-550.43
Rugut arcus	-4783.7	-641.88	-3683.21	-90.83
Rugut felix	-17038	-637.73	-0.4	-151.7
Scabr planetensis	-15759.5	-650.29	-1351.05	-278.37
Silta dilcheri	-16116.9	-657.3	-3223.84	-278.37
Spiro spiralis	-18077.2	-659.93	-1471.13	-203.77
Stria catatumbus	-17817.3	NA	-789.04	-97.29
Stria poloreticulatu	-10086.6	-659.93	-0.1513	-386.52
Stria saccolomoides	-16169.7	-537.29	-563.571	-90.83
Tetra maculosus	-17625.2	-662.33	-1351.05	-107.94
Tetra transversalis	-18249.3	-662.33	-727.52	NA
Trico clarensis	-18077.2	-644.25	-7790.69	-251.53
Trico finitus	-15878.6	-638.33	-194.688	-403.39
Tuber vancampoae	-9411.42	-468.84	-1894.29	-409.52
Tuber verrucatus	-17815.1	-645.6	-3655.35	-99.53
Venez distinctus	-16867.7	-550.43	-14429.1	-550.43
Verru etayoi	-16114.7	-641.88	-3742.15	-145.35
Verru rotundiporus	-14964	-659.93	-1317.26	-90.83
Verru rugulatus	-17458	-614.35	-10775.9	-372.38
Zonoc ramonae	-17372.7	-645.6	-817.278	NA

9.1. c). Events of wells 1-AS-105-AM and 1-AS-4a-AM (Hoorn *et al.* 1993). FL EM= Early Miocene Flooding, FL MM = Middle Miocene Flooding. Ramón (not confirmed) is the Formation underlying the Solimões Formation; Quaternary is the top section recent deposits.

<b>Taxa</b>	<b>FAD105</b>	<b>FAD4a</b>	<b>LAD105</b>	<b>LAD4a</b>
Bomba baculatus	-325.3	-131	NA	NA
Bomba muinaneorum	-370.3	-236.5	-35.4	-59
Bomba nacimientoensi	NA	-236.5	-35.4	-59
Crass columbianus	NA	-273.6	-39.8	-59
Crass vanraadshooven	-360.9	-181.85	-34.6	NA
Croto annemariae	-267.9	-238.6	-110.7	NA
Echip akanthos	NA	-273.6	NA	-34.2

Echip estelae	-370.3	-75.2	NA	-75.2
Echit spinosus	-324.9	-143.1	-34.6	-89
FL EM	-293.3	115	-284	65
Grims magnaclavata	-326.2	-89	NA	NA
Heter rotundus	-326.2	-263.5	NA	-75.2
Malva maristellae	-250	-229.8	-34.6	-34.2
Margo vanwijhei	-370.3	-218.2	NA	-78.9
Multi vanderhammenii	-267.9	-59	-30	-59
Perfo digitatus	-298.9	-272.6	-34.6	NA
Polya mariae	-298.9	-238.6	-44.7	-142.9
Proxa tertiaria	-370.3	-238.6	-34.6	-44.75
Psila devriesii	NA	NA	-79.9	-75.2
Psila herngreenii	-359	-238.6	-53	-44.75
Psila obesus	-230.2	-191.2	NA	-34.2
Psila redundantis	-325.3	-272.6	-39.8	NA
Psila silvaticus	NA	NA	-30	-44.75
Quaternary	-20	-15	NA	NA
Ramon	-405	-353	-330	-338
Ranun operculatus	-370.3	NA	NA	-44.75
Retim absyae	-283.2	-238.6	-30	NA
Retis crassiannulatu	-325.3	-273.6	-75.3	-59
Retit caputoi	-326.2	NA	-79.9	-131
Retit crassicostatus	-125.3	-263.5	-44.7	NA
Retit irregularis	-370.3	NA	NA	-75.2
Retit kaarsii	-359	-267	-39.8	-34.2
Retit lorenteae	-272.1	-59	NA	NA
Solimoes	-330	-338	-20	-15
Spiro spiralis	-250	-181.85	-44.7	-125.2
Stria catatumbus	-165.5	-267	NA	NA
Verru rotundiporus	-26.35	NA	NA	-44.75

9.1. d). Events of wells 1-AS-105-AM and 1-AS-27-AM (Silva-Caminha *et al.* 2010). Species with “ ” are informal.

<b>Taxa</b>	<b>FAD105</b>	<b>FAD27</b>	<b>LAD105</b>	<b>LAD27</b>
Areci regio	-370.3	NA	-30	-49.6
Bomba araracuarensis	-161.7	-354.5	-39.8	-43.7
Bomba baculatus	-325.3	-264.3	NA	-216
Bomba brevis	-324.9	-354.5	-69.8	NA
Bomba muinaneorum	-370.3	-216	-35.4	-43.7
Cicho longispinosus	-165.5	-354.5	-30	NA
Clava microclavatus	-324.6	-233.1	-30	-43.7
Crass columbianus	NA	-280.2	-39.8	-57.9
Crass vanraadshooven	-360.9	-354.5	-34.6	-49.6

Croto reticulatus	-359	-354.5	-30	NA
Cteno suigeneris	-359	-284.5	-34.6	-63.6
Echin muelleri	-267.9	-301.8	NA	-150.7
Echip estelae	-370.3	-216	NA	NA
Echip intectatus	-272.1	-97.8	-34.6	-97.8
Echip jutaiensis	-230.2	-216	-35.4	-43.7
Echip lophatus	-289.9	-233.1	NA	-63.6
Echit spinosus	-324.9	-150.7	-34.6	-150.7
Foveo ornatus	-324.9	-192	-34.6	-53.7
Grims magnaclavata	-326.2	NA	NA	-43.7
Heter incomptus	-325.3	-301.8	-34.6	-53.7
Heter rotundus	-326.2	-301.8	NA	-53.7
Heter verrucosus	-289.9	-354.5	NA	NA
Ilexp tropicalis	-324.9	-216	-34.6	-216
Jandu minor	-370.3	NA	-165.5	NA
Jandu seamrogiformis	-284	-264.3	-35.4	-264.3
Ladak caribbiensis	-187.6	-221	-34.6	NA
Laevi granulatus	-324.9	-161.2	NA	-161.2
Magna grandiosus	-359	-354.5	-34.6	NA
Malva maristellae	-250	-57.9	-34.6	-43.7
Margo vanwijhei	-370.3	-137	NA	-53.7
Mauri franciscoimin	-325.3	NA	NA	-43.7
Monop annulatus	NA	-354.5	NA	NA
Multi vanderhammenii	-267.9	-43.7	-30	-43.7
Parso brenacii	-298.9	-143.1	-44.7	-53.7
Perfo digitatus	-298.9	-301.8	-34.6	-54.3
Polyp planus	-210.1	-354.5	NA	-49.6
Polyp pseudopsilatus	-155.1	-53.7	-35.4	-53.7
Prote triangulatus	-370.3	-303	-30	-54.3
Proxa tertiaria	-370.3	-233.1	-34.6	-49.6
Psila devriesii	NA	NA	-79.9	-264.3
Psila fissilis	-298.9	-264.3	NA	-221
Psila herngreenii	-359	-264.3	-53	NA
Psila nanus	-359	-216	-69.8	-216
Psila triangularis	-299.3	NA	-79.9	-301.8
Pteri gemmatus	-254.3	-43.7	-91.5	-43.7
Ranun operculatus	-370.3	-301.8	NA	NA
Retib retibolus	-210.1	-303	NA	-137
Retib yavarensis	-182	-354.5	-161.7	-49.6
Retim absyae	-283.2	NA	-30	NA
Retis crassiannulatu	-325.3	NA	-75.3	-54.3
Retit irregularis	-370.3	-354.5	NA	-53.7
Retit simplex	-370.3	-284.5	-140.9	-53.7
Retit traversei	-44.7	-216	-44.7	-137
Rugut arcus	-30	-284.5	-30	-284.5
Silta dilcheri	-267.9	-216	-39.8	-136.6



Solimoes	-330	-378	-20	-13
Spiro spiralis	-250	-354.5	-44.7	NA
Stria anastomosatus	-324.9	-192	-34.6	-136.6
Stria catatumbus	-165.5	-354.5	NA	-43.7
Stria poloreticulatu	-364.8	-354.5	NA	-137
Verru etayoi	-324.3	-192	-51.6	-192
Verru rotundiporus	-26.35	-280.2	NA	-67.9

9.1. e). R codes to produce LOC equations (= intercepts and slopes for various segments in each correlation). Equation results are shown within the codes (in bold). In all codes, Medina is the reference section, which therefore becomes the composite section. Codes written by Jaramillo *et al.* (2011).

```
##code to transfer Saltarin values into Medina values. Saltarin values in first
#column(depend variable)
locMolino<-read.table("LOC_SaltarinvsMedina.txt",header=T,sep="\t",na.strings =
"NA")##contains the calibration points between both sites, in first column goes the dependent
variable
locMolino = locMolino[order(locMolino$saltarin),]##PMedina ordered from young to old

##Loops that will produce all intercepts and coeff for calibration
intercept.molino <- numeric (nrow(locMolino)-1)
slope.molino <- numeric (nrow(locMolino)-1)
for (i in (1:(nrow(locMolino)-1))) {
segcal.molino=lm(locMolino$medina[i:(i+1)]~locMolino$saltarin[i:(i+1)])## need to change,
first independent
intercept.molino[i]=segcal.molino$coefficients[1]
slope.molino[i]=segcal.molino$coefficients[2]
}

#intercepts for composite section and well saltarin:
[1] 1748.4964 1650.9603 -503.0868 1553.3205 2137.8087 -525.7042
[7] -19885.2057 -11199.5390 -90596.3240 -9934.3806 -8350.9091 -4226.5144
[13] 3702.3409

#slopes for composite section and well Saltarin:
[1] 5.104830 5.650334 10.746379 6.308920 5.118516 10.239573
[7] 46.105778 30.342890 159.915292 30.202429 27.705628 21.318644
[13] 9.206125

calibfun.molino=function(a,b) { ##lm for any given segment, a is taus, b is segment to use
c=a*slope.molino[b]+ intercept.molino[b]
```

```

c
}

slopesegmentfun.molino=function(b) {
a=numeric (nrow(locMolino)-1)
segment=numeric(1)
for (i in (1:(nrow(locMolino)-1))) {
a[i]=ifelse(b>=locMolino[i,1] & b<locMolino[(i+1),1],which(locMolino ==
locMolino[i,1]),0)##gives back the segment number
segment=which (a >0)
}
segment
}

molinoformcomposite=read.table("Saltarin_UnknownAges.txt",header=F,sep="\t",na.strings =
"NA")#the depths that we need to translate into composite units
molinoformcomposite=as.matrix(molinoformcomposite)
segmenttouse.molino=as.numeric(apply(molinoformcomposite,1,slopesegmentfun.molino))
write.table(calibfun.molino(molinoformcomposite, segmenttouse.molino), file =
"saltarinTOMedina.csv", sep = ",", col.names = NA, qmethod = "double")##saltarin expressed in
Medina units (or composite units)

-----

##code to transfer 105AM values into Medina values. 105AM values in first column(depend
#variable)
locMolino<-read.table("LOC_105AMvsMedina.txt",header=T,sep="\t",na.strings = "NA")##contains
the calibration points between both sites, in first column goes the dependent variable
locMolino = locMolino[order(locMolino$X1.AS.105.AM.m),]##PMedina ordered from young to old

##Loops that will produce all intercepts and coeff for calibration
intercept.molino <- numeric (nrow(locMolino)-1)
slope.molino <- numeric (nrow(locMolino)-1)
for (i in (1:(nrow(locMolino)-1))) {
segcal.molino=lm(locMolino$Medina[i:(i+1)]~locMolino$X1.AS.105.AM.m[i:(i+1)])## need to
change, first independent
intercept.molino[i]=segcal.molino$coefficients[1]
slope.molino[i]=segcal.molino$coefficients[2]
}

calibfun.molino=function(a,b) { ##lm for any given segment, a is taus, b is segment to use
c=a*slope.molino[b]+ intercept.molino[b]
c
}

```

```
#intercepts for composite section and well 1-AS-105-AM:
[1] 3468.82496 3082.37073 3357.69671 3504.48858 -1641.30022 3273.91719
[7] 2265.23883 3220.17700 2305.77440 2752.46484 3126.09072 2944.64659
[13] -5799.04220 5464.31808 -17.37225 -5650.92786 2849.71214 -8962.01604
[19] 5619.39754 8946.81255 91.53890 -1564.43957 -1567.52472 7958.94373
[25] 7958.88723 7283.46514

#slopes for composite section and well 1-AS-105-AM:
[1] 7.1462776 14.5213583 9.3265285 7.1024092 75.4395780 10.5950211
[7] 20.9830578 11.9235250 19.5435467 16.0434962 13.2552434 14.5378060
[13] 67.3697624 0.3259512 32.4147086 62.0650013 19.7732600 71.1759798
[19] 12.6630842 0.9509581 31.7759266 37.4219494 37.4323463 5.6031835
[25] 5.6033623 7.6841451
```

```
slopesegmentfun.molino=function(b) {
a=numeric (nrow(locMolino)-1)
segment=numeric(1)
for (i in (1:(nrow(locMolino)-1))) {
a[i]=ifelse(b>=locMolino[i,1] & b<locMolino[(i+1),1],which(locMolino ==
locMolino[i,1]),0)##gives back the segment number
segment=which (a >0)
}
segment
}
```

```
molinoformcomposite=read.table("105AM_UnknownAges.txt",header=F,sep="\t",na.strings = "NA")
molinoformcomposite=as.matrix(molinoformcomposite)
segmenttouse.molino=as.numeric(apply(molinoformcomposite,1,slopesegmentfun.molino))
write.table(calibfun.molino(molinoformcomposite, segmenttouse.molino), file =
"105AMTomedina.csv", sep = ",", col.names = NA, qmethod = "double")##105AM into Medina units
```

9.1. f). R codes to transfer composite units to geological time. This code uses a file “calibration\_2011December.txt” from Jaramillo *et al.* (2011).

```
##COMPOSITE UNITS TO GEOLOGIC TIME
calibration<-read.table("calibration_2011December.txt",header=T,sep="\t",na.strings =
"NA")##contains the calibration points
calibration = calibration[order(calibration $CU),]##composite units ordered from young to old

plot(calibration$CU,calibration$time,xlab="composite units",ylab="time (My)", pch=19)

##Loops that will produce all intercepts and coeff for calibration
intercept <- numeric (nrow(calibration)-1)
slope <- numeric (nrow(calibration)-1)
```

```

for (i in (1:(nrow(calibration)-1))) {
segcal=lm(calibration$time[i:(i+1)]~calibration$CU[i:(i+1)])
intercept[i]=segcal$coefficients[1]
slope[i]=segcal$coefficients[2]
}

calibfun=function(a,b) { ##lm for any given segment, a is composite unit, b is segment to
use
c=a*slope[b]+ intercept[b]
c
}

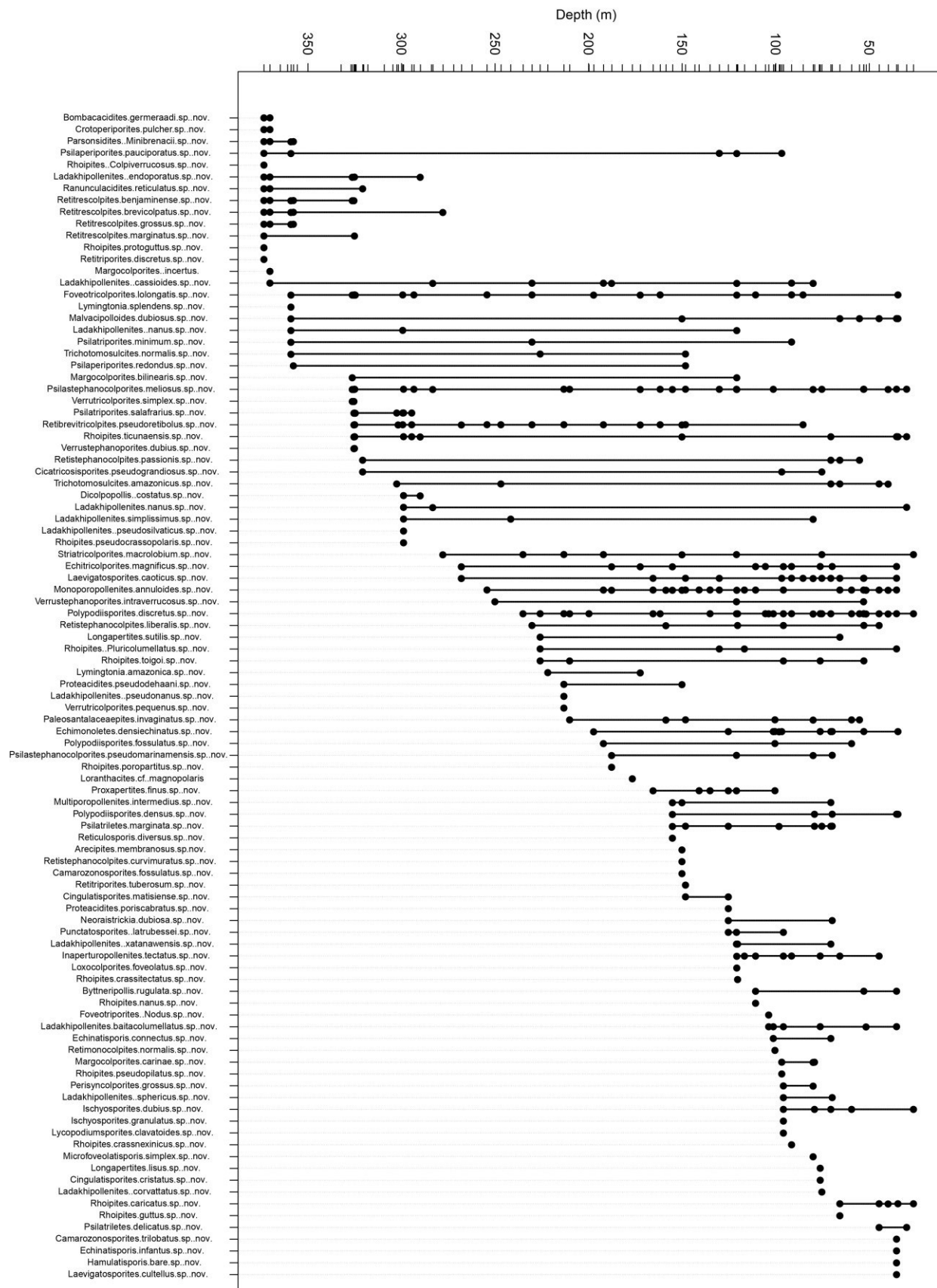
##function that gives back the segment number
slopesegmentfun=function(b) {
a=numeric (nrow(calibration)-1)
segment=numeric(1)
for (i in (1:(nrow(calibration)-1))) {
a[i]=ifelse(b>=calibration[i,1] & b<calibration[(i+1),1],which(calibration ==
calibration[i,1]),0)##gives back the segment number
segment=which (a >0)
}
segment
}

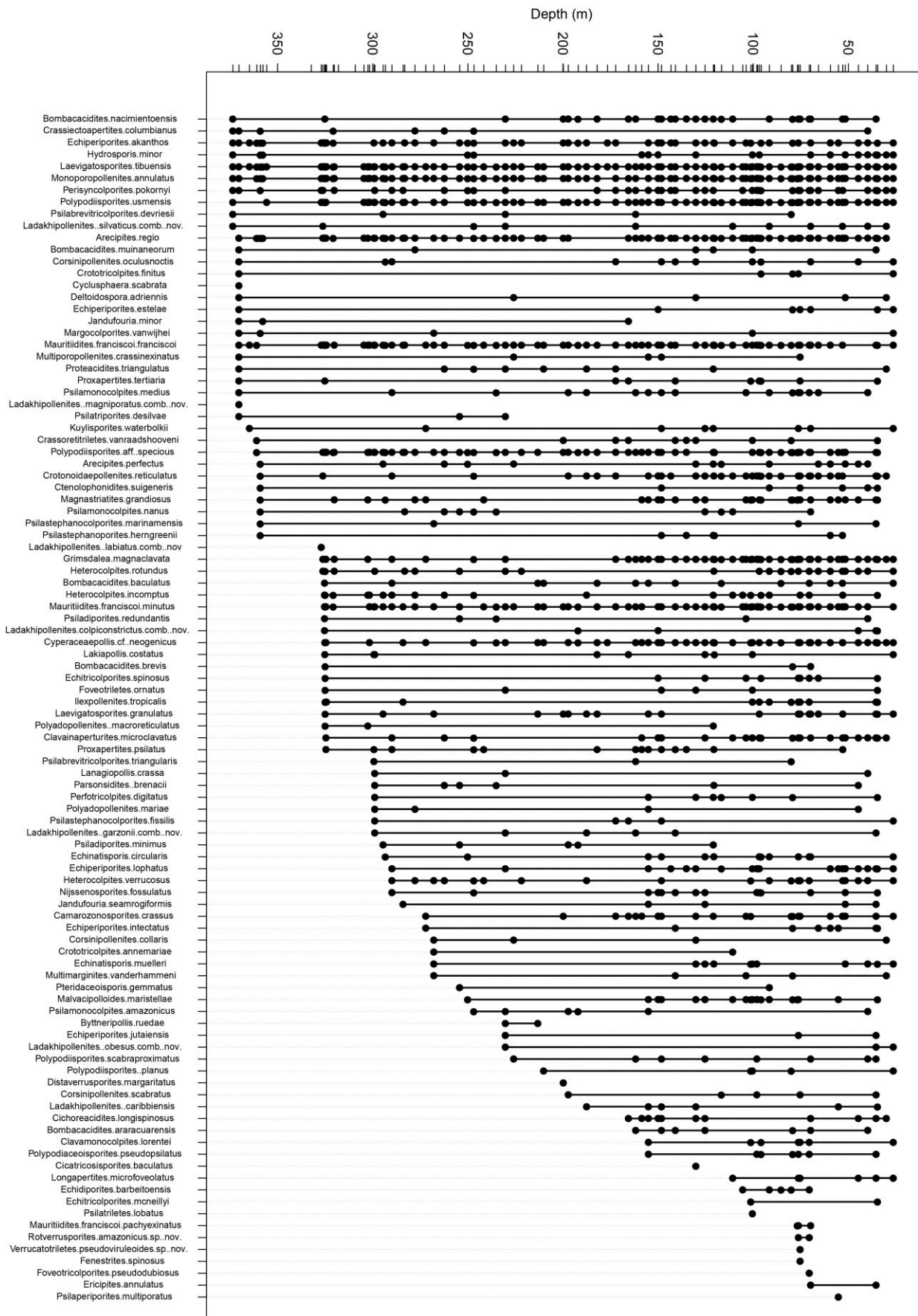
compositeunits<-as.matrix(read.table("105AM_CU.txt",header=F,sep="\t",na.strings =
"NA"))##the composite units to be transformed into time
segmenttouse=as.numeric(apply(compositeunits,1,slopesegmentfun))## apply to find the segment
for each composite unit, eg.
timeunits=calibfun(compositeunits, segmenttouse)##calculate the time for each composite unit
plot(compositeunits, timeunits)
write.table(timeunits, file = "105AM_timeunits.csv", sep = ",", col.names = NA, qmethod =
"double")

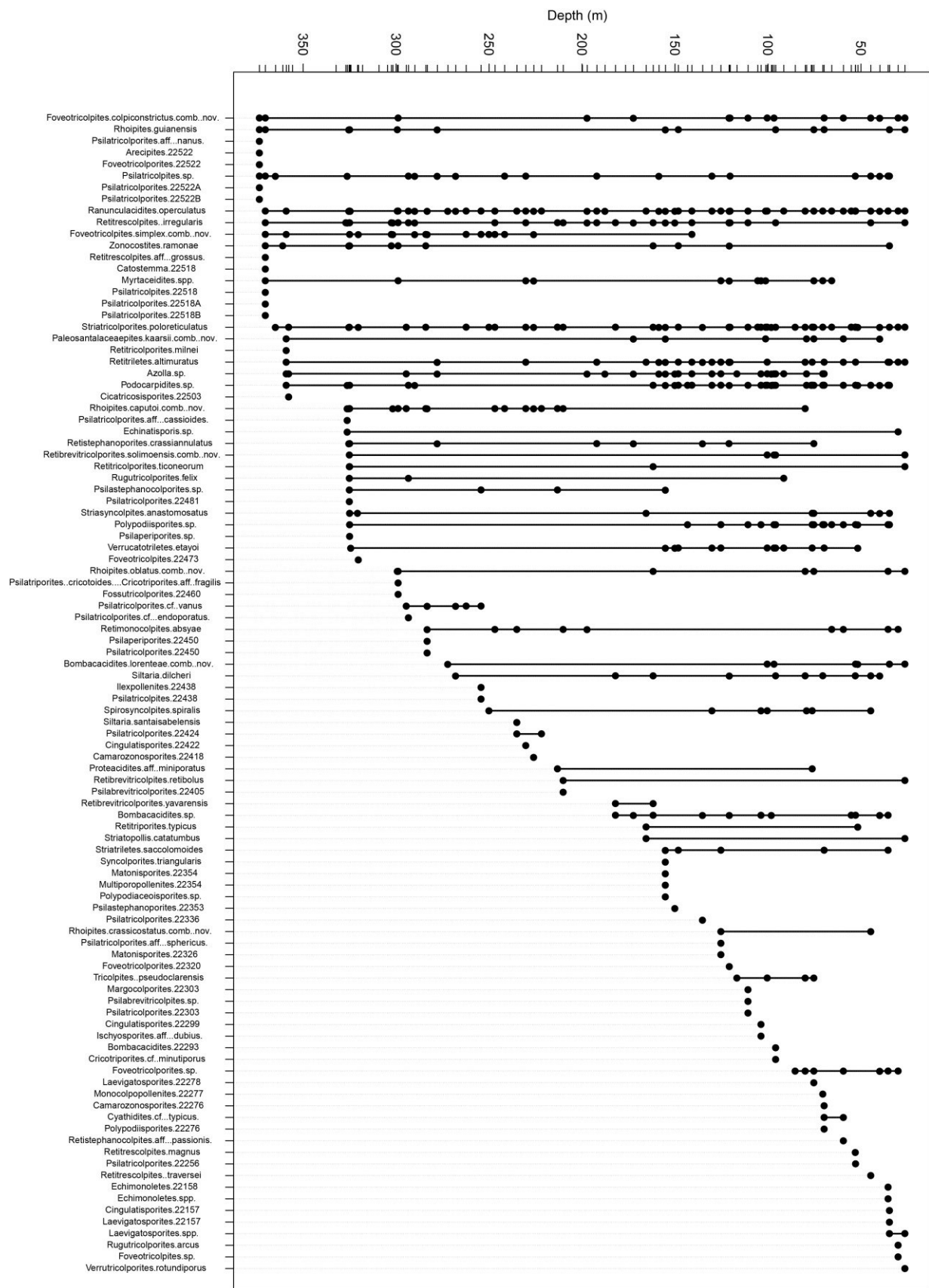
compositeunits<-as.matrix(read.table("Saltarin_CU.txt",header=F,sep="\t",na.strings =
"NA"))##the composite units to be transformed into time
segmenttouse=as.numeric(apply(compositeunits,1,slopesegmentfun))## apply to find the segment
for each composite unit, eg.
timeunits=calibfun(compositeunits, segmenttouse)##calculate the time for each composite unit
plot(compositeunits, timeunits)
write.table(timeunits, file = "saltarin_timeunits.csv", sep = ",", col.names = NA, qmethod =
"double")

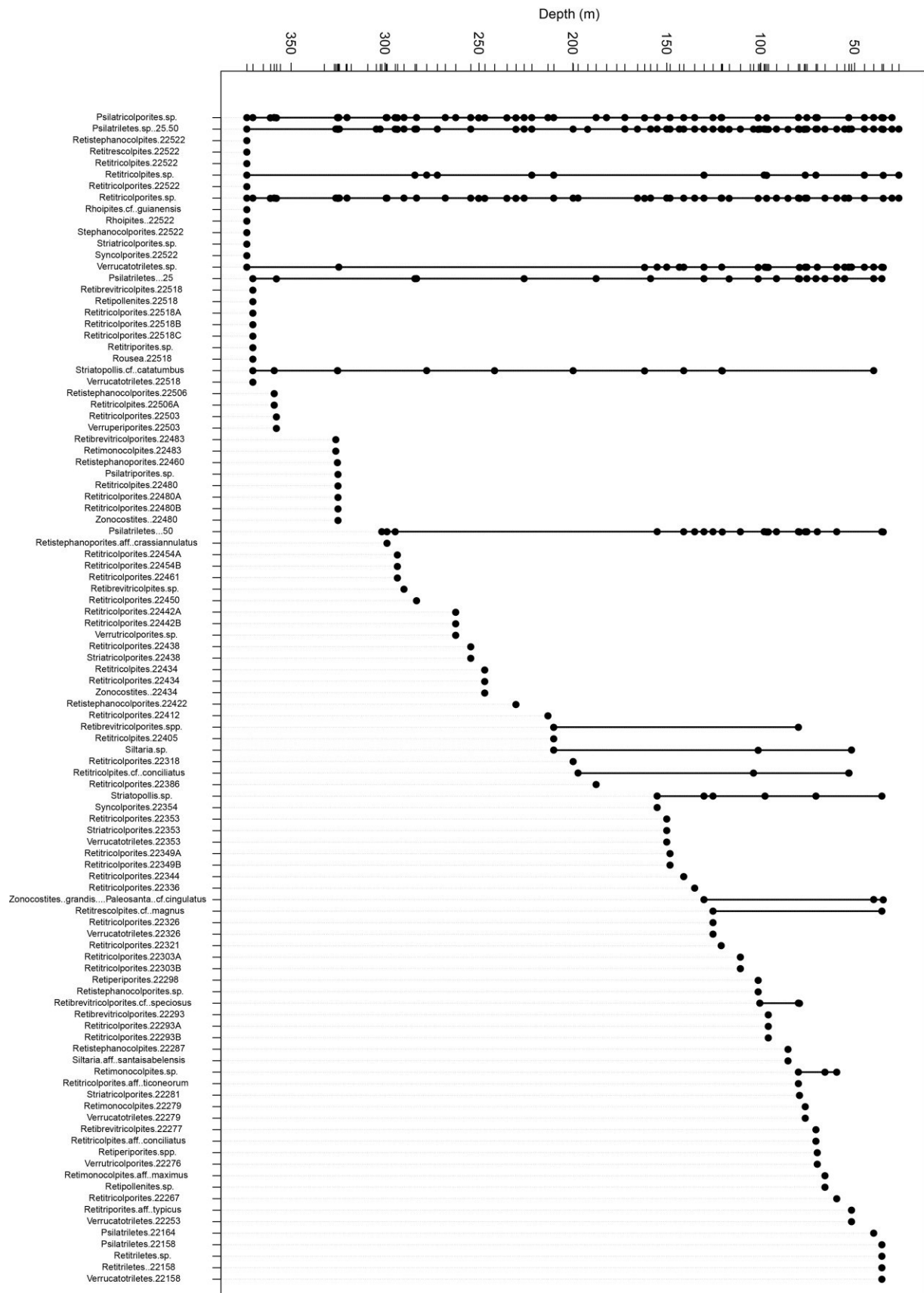
```

9.1.g) Range charts with pollen counts from core 1-AS-105-AM (ordered by FAD).











## 9.2. Table with all known botanical affinities (Chapter 6).

taxa name	type	family/ subfamily	genus/ species	life habit	ecology	author
Multimarginites vanderhammeni	pollen	Acanthaceae	Trichanthera/ Bravaisia	tree	terra firme	Germeraad et al. 1968
Retitrescolpites? traversei	pollen	Acanthaceae	Teliostachya	tree	lowland	Silva-Caminha et al 2010
Echiperiporites akanthos	pollen	Alismataceae	Sagittaria/ Echinodorus	herb	swamp, lake	This study
Proxapertites tertiaria	pollen	Annonaceae	Crematosperma	tree	lowland	Van der Hammen and Garcia Mutis 1965
Ctenolophonidites suigeneris	pollen	Apocynaceae	Geissospermum	tree	terra firme	Silva-Caminha et al 210
Dicolpopollis? "costatus"	pollen	Apocynaceae	Macoubea	tree	terra firme	This study
Margocolporites "carinae"	pollen	Apocynaceae	Aspidosperma	tree	terra firme	This study
Psilastephanoporites herngreenii	pollen	Apocynaceae	unknown	tree	unknown	Hoorn 1993
Verrustephanoporites "intraverrucosus"	pollen	Apocynaceae	Forteronia/ Prestonia/ Odontadenia	lowland liana	lowland forest	Dessaune-Rodrigues et al 2016
Ilexpollenites 22438	pollen	Aquafoiliaceae	Ilex	tree	terra firme, white-sand	Thiergart 1937 ex Potonie 1960
Ilexpollenites tropicalis	pollen	Aquafoiliaceae	Ilex	tree	terra firme, white-sand	Silva-Caminha et al 2010, Thiergart 1937 ex Potonie 1960
Rhoipites ticunaensis	pollen	Araliaceae	Schefflera	tree	lowland	This study
Cyclusphaera scabrata	pollen	Araucariaceae	unknown	tree	montane	Jaramillo and Dilcher 2001
Arecipites "membranous"	pollen	Arecaceae	unknown	tree	unknown	This study
Arecipites 22522	pollen	Arecaceae	unknown	tree	unknown	This study
Arecipites perfectus	pollen	Arecaceae	unknown	tree	unknown	Silva-Caminha et al 2010
Arecipites regio	pollen	Arecaceae	unknown	tree	unknown	Van der Hammen and Garcia, 1966
Clavamonocolpites lorentei	pollen	Arecaceae	Iriarte(?)	tree	terra firme	Gonzalez 1967
Echidiporites barbeitoensis	pollen	Arecaceae	Korthalsia ferox	tree	terra firme	Muller et al 1987
Grimsdalea magnaclavata	pollen	Arecaceae	extinct genus	tree	unknown	Germeraad et al. 1968
Longapertites microfoveolatus	pollen	Arecaceae	unknown	tree	unknown	Jaramillo and Rueda 2013
M. franciscoi pachyexinatus	pollen	Arecaceae	Mauritia/ Mauritiella	tree	varzea, swamp	(Van der Hammen 1956) Van Hoeken-Klinkenberg 1964
Mauritiidites franciscoi franciscoi	pollen	Arecaceae	Mauritia	tree	varzea, swamp	(Van der Hammen 1956) Van Hoeken-Klinkenberg 1964
Mauritiidites franciscoi minutus	pollen	Arecaceae	Mauritia	tree	varzea, swamp	(Van der Hammen 1956) Van Hoeken-Klinkenberg 1964
Psilamonocolpites amazonicus	pollen	Arecaceae	Euterpe	tree	lowland	Hoorn 1993
Psilamonocolpites medius	pollen	Arecaceae	unknown	tree	lowland	(Van der Hammen 1956) Van der Hammen and Garcia 1966
Psilamonocolpites nanus	pollen	Arecaceae	unknown	tree	lowland	Hoorn 1993
Trichotomosulcites "amazonicus"	pollen	Arecaceae	unknown	tree	lowland	This study
Trichotomosulcites "normalis"	pollen	Arecaceae	unknown	tree	lowland	This study
Longapertites "lisus"	pollen	Arecaceae (?)	unknown	tree	unknown	This study
Longapertites "sutilis"	pollen	Arecaceae (?)	unknown	tree	unknown	This study
Cichoreacidites longispinosus	pollen	Asteraceae	unknown	herb	bars, swamps, savannahs	Lorente 1986
Echitricolporites mcneillyi	pollen	Asteraceae	unknown	herb	bars, swamps, savannahs	Germeraad et al. 1968
Echitricolporites spinosus	pollen	Asteraceae	unknown	herb	bars, swamps, savannahs	Germeraad et al. 1968
Fenestrites spinosus	pollen	Asteraceae	unknown	herb	bars, swamps, savannahs	Van der Hammen 1956 ex Lorente, 1986
Ladakhipollenites? silvaticus	pollen	Burseraceae/ Sapotaceae	unknown	tree	unknown	Hoorn 1993
Rugutricolporites arcus	pollen	Chrysobalanaceae	Licania	tree	lowland	Hoorn 1993
Clavainaperturites microclavatus	pollen	Cloranthaceae	Hedyosmum	tree	montante, riparian forests in cerrados	Hoorn et al 1994, D'Apolito et al 2013
Lyningtonia "splendens"	pollen	Convolvulaceae	Evolvulus/ Jacquemontia	herb	lowland liana	This study
Perfotricolpites digitatus	pollen	Convolvulaceae	Merremia	herb	lowland liana	Gonzalez 1967
Echiperiporites lophatus	pollen	Convolvulaceae (?)	unknown	herb	liana?	This study

Cyperaceapollis cf. neogenicus	pollen	Cyperaceae	unknown	herb	bars, swamps, savannahs	Krutzsch 1970
Ericipites annulatus	pollen	Ericaceae	unknown	unknown	unknown	Gonzalez 1967
Crototricolpites annemariae	pollen	Euphorbiaceae	Croton	tree	terra firme, montane	Leidelmeyer 1966
Foveotricolpites simplex	pollen	Euphorbiaceae	Sapium	tree	lowland	Gonzalez 1967
Ladakhipollenites? caribbiensis	pollen	Euphorbiaceae	Sapium	tree	terra firme, varzea	Muller et al. 1987
Ranunculacidites operculatus	pollen	Euphorbiaceae	Alchornea	tree	lowland, varzea	(Van der Hammen & Wymstra, 1964) Jaramillo & Dilcher 2001
Retitrescolpites? irregularis	pollen	Euphorbiaceae	Amanoa	tree	lowland	(Van der Hammen & Wymstra 1964) Jaramillo & Dilcher 2001
Ladakhipollenites? cassioides	pollen	Fabaceae, Caesalpinioideae	Cacia?	tree	unknown	This study
Margocolporites vanwijhei	pollen	Fabaceae, Caesalpinioideae	Caesalpineae	tree	terra firme	Germeraad et al. 1968
Psilatriporites desilvae	pollen	Fabaceae, Caesalpinioideae	unknown	tree	lowland	Hoorn 1993
Striatopollis catatumbus	pollen	Fabaceae, Caesalpinioideae	unknown	tree	lowland	(Gonzalez 1967) Takahashi and Jux 1989
Striatricolporites "macrolobium"	pollen	Fabaceae, Caesalpinioideae	unknown	tree	lowland	This study
Polyadopollenites mariae	pollen	Fabaceae, Mimosoideae	Acacia	tree	lowland	Dueñas 1980
Crassiectoapertites columbianus	pollen	Fabaceae, Papilionoideae	unknown	tree	terra firme	Dueñas 1980
Ladakhipollenites? magniporatus	pollen	Fabaceae?	unknown	unknown	unknown	Hoorn 1993
Polyadopollenites macroreticulatus	pollen	Hippocrateaceae	Hippocratea (volubilis?)	tree	lowland	Salard-Cheboldaeff 1974
Psilabrevitricolporites devriesii	pollen	Humiriaceae	Humiria	tree	lowland, montane, white-sand	Lorente 1986
Loranthacites cf. "magnopolaris"	pollen	Loranthaceae	unknown	tree	unknown	Jaramillo and Rueda 2013
Verrutricolporites rotundiporus	pollen	Lythraceae	Crenea	tree	lowland	Van der Hammen and Wymstra 1964
Perisyncolporites pokomyi	pollen	Malpighiaceae	unknown	unknown	lowland	Germeraad et al 1968
Bytneripollis ruedae	pollen	Malvaceae	Bytneria	tree	terra firme	Silva-Caminha et al 210
Catostemma 22518	pollen	Malvaceae	Catostema	tree	terra firme	
Jandufouria minor	pollen	Malvaceae	Catostema (?)	tree	terra firme, varzea	Germeraad et al. 1968
Jandufouria seamrogiformis	pollen	Malvaceae	Catostema	tree	terra firme, varzea	Germeraad et al. 1968
Retistephanoporites crassiannulatus	pollen	Malvaceae	Quararibea	tree	lowland	Lorente 1986, Roubik and Moreno 1991
Malvacipolloides "dubiosus"	pollen	Malvaceae (?)	unknown	unknown	unknown	This study
Bombacidites "germeradii"	pollen	Malvaceae, Bombacoideae	unknown	tree	unknown	
Bombacidites 22293	pollen	Malvaceae, Bombacoideae	unknown	tree	unknown	
Bombacidites araracuarensis	pollen	Malvaceae, Bombacoideae	Ceiba sp	tree	terra firme, varzea	Hoorn 1994
Bombacidites baculatus	pollen	Malvaceae, Bombacoideae	Pachira aquatica	tree	terra firme, swamp	Muller et al. 1987
Bombacidites brevis	pollen	Malvaceae, Bombacoideae	unknown	tree	unknown	(Dueñas, 1980) Muller et al., 1987
Bombacidites lorenteae	pollen	Malvaceae, Bombacoideae	Bombax	tree	varzea	Hoorn 1993
Bombacidites muinaneorum	pollen	Malvaceae, Bombacoideae	Bombacopsis	tree	terra firme, varzea	Hoorn 1993
Bombacidites nacimientoensis	pollen	Malvaceae, Bombacoideae	Bombax	tree	terra firme, varzea	Anderson 1960, Elsik 1968
Bombacidites sp.	pollen	Malvaceae, Bombacoideae	unknown	tree	unknown	
Malvacipolloides maristellae	pollen	Malvaceae, Bombacoideae	unknown	tree	terra firme	Muller et al. 1987
Echiperiporites estelae	pollen	Malvaceae/ Convolvulaceae	unknown	unknown	unknown	Germeraad et al. 1968
Heterocolpites incomptus	pollen	Melastomataceae	unknown	tree	terra firme	Hoorn 1993
Heterocolpites rotundus	pollen	Melastomataceae	unknown	tree	terra firme	Hoorn 1993
Heterocolpites verrucosus	pollen	Melastomataceae	unknown	tree	terra firme	Hoorn 1993
Psiladiporites minimus	pollen	Moraceae	Ficus/ Artocarpus/ Sorocea	tree	lowland	Van der Hammen & Wymstra 1964
Psiladiporites redundantis	pollen	Moraceae	unknown	tree	lowland	Gonzalez 1967

Psilatropites "minimum"	pollen	Moraceae	unknown	tree	lowland	This study
Retimonocolpites absyae	pollen	Myristicaceae	Virola	tree	lowland, varzea	Hoon 1993
Myrtacidites spp.	pollen	Myrtaceae	Myrtaceae	tree	lowland	This study
Corsinipollenites collaris	pollen	Onagraceae	Ludwigia	herb	swamp, lake	(Thiergart 1940); Nakoman 1965
Corsinipollenites oculusnotis	pollen	Onagraceae	Ludwigia	herb	swamp, lake	(Thiergart 1940); Nakoman 1965
Corsinipollenites scabratus	pollen	Onagraceae	Ludwigia	herb	swamp, lake	(Thiergart 1940); Nakoman 1965
Retistephanocolpites "passionis"	pollen	Passifloraceae	Passiflora	herb	lowland liana	This study
Lanagiopollis crassa	pollen	Pellicieraceae	Pelliciera	tree	mangrove	Jaramillo and Rueda 2013
Monoporopollenites "annuloides"	pollen	Poaceae	unknown	herb	bars, swamps, savannahs	This study
Monoporopollenites annulatus	pollen	Poaceae	unknown	herb	bars, swamps, savannahs	(Van der Hammen, 1954) Jaramillo & Dilcher 2001
Podocarpidites sp.	pollen	Podocarpaceae	Podocarpus	tree	lowland, montane	Punyasena et al 2011, D'Apolito et al in prep
Psilastephanocolporites fissilis	pollen	Polygalaceae	Polygala	herb	swamp, lake	Lorente 1986
Zonocostites ramonae	pollen	Rhizophoraceae	Rhizophora	tree	mangrove	Dueñas 1980
Proteacidites triangulatus	pollen	Sapindaceae/ Proteaceae	unknown	tree	lowland	Lorente 1986
Psilabrevitricolporites triangularis	pollen	Sapindaceae?	unknown	unknown	unknown	Lorente 1986
Ladakhipollenites? obesus	pollen	Sapotaceae	unknown	tree	lowland	Hoon 1993
Psilastephanocolporites marinamensis	pollen	Sapotaceae	unknown	tree	lowland	Hoon 1994
Ladakhipollenites? labiatus	pollen	Sapotaceae, Pouteria	unknown	tree	lowland	Hoon 1993
Ladakhipollenites? pseudosilvaticus	pollen	Sapotaceae?	unknown	tree	unknown	This study
Rhoipites guianensis	pollen	Tiliaceae/ Sterculiaceae	unknown	tree	lowland	(Van der Hammen & Wymstra 1964) Jaramillo & Dilcher 2001
Nijssenosporites fossulatus	spore	Adiantaceae	Pityrogramma	fern	lowland	Jaramillo and Rueda 2013
Cicatricosisporites baculatus	spore	Anemiaceae	Anemia	fern	terra firme	Regali et al 1974
Cyathidites cf. "typicus"	spore	Cyatheaceae	unknown	fern	unknown	Couper 1953
Kuylisporites waterbolkii	spore	Cyatheaceae	Cyathea horrida	fern	montane	Potonie 1956
Lycopodiumsporites "clavatooides"	spore	Lycopodiaceae (?)	unknown	fern	unknown	This study
Distaverrusporites margaritatus	spore	Ophioglossaceae (?), Lindsaeaceae (?)	unknown	fern	unknown	Jaramillo and Rueda 2013
Polypodiisporites aff. speciosus	spore	Polypodiaceae	unknown	fern	lowland	Sah 1967
Polypodiisporites usmensis	spore	Polypodiaceae, Blechnaceae	unknown	fern	unknown	(Van der Hammen, 1956a) Khan and Martin 1972
Deltoidospora adriennis	spore	Pteridaceae	Acrostichum aureum	fern	swamp, mangrove	(Potonie & Gelletich 1933) Frederiksen
Magnastriatites grandiosus	spore	Pteridaceae	Ceratopteris	fern	aquatic	(Kedves & Sole de Porta 1963) Dueñas 1980
Polypodiaceoisporites pseudopsilatus	spore	Pteridaceae	Pteris	fern	lowland	Jaramillo and Rueda 2013
Azolla sp.	spore	Salviniaceae	Azolla	fern	aquatic	
Hydrosporis minor	spore	Salviniaceae	Salviniaceae, Salvinia	fern	aquatic	Silva-Caminha et al 2010
Crassoretitrites vanraadshooveni	spore	Schizaceae	Lygodium microphyllum	fern	swamp	Germeraad et al. 1968
Cingulatisporites "cristatus"	spore	Selaginellaceae	Selaginella	fern	unknown	This study
Echinatisporis "connectus"	spore	Thelypteraceae/ Athyriaceae/ Marathiaceae	unknown	fern	unknown	Krutzsch 1967
Echinatisporis "infantus"	spore	Thelypteraceae/ Athyriaceae/ Marathiaceae	unknown	fern	unknown	Krutzsch 1967
Echinatisporis circularis	spore	Thelypteraceae/ Athyriaceae/ Marathiaceae	unknown	fern	unknown	Krutzsch 1967
Echinatisporis muelleri	spore	Thelypteraceae/ Athyriaceae/ Marathiaceae	unknown	fern	unknown	Krutzsch 1967
Echinatisporis sp.	spore	Thelypteraceae/ Athyriaceae/ Marathiaceae	unknown	fern	unknown	Krutzsch 1967

9.3. R scripts for all figures and analyses (organised by chapter), except scripts for the age model that are in Appendix Tables 9.1. (Excel files are stored in the electronic supplement of this thesis – CD).

### 9.3.1 - Chapter 1 (Introduction), Fig. 1.1 and 1.2:

```
data<-read.csv("zachos2008.csv",head=T)
plot(data$Age,data$d180.5pt,xlim=c(0,65), ylim=c(5,-1),type="l",col="blue",lwd=1.5,
ylab="d180",xlab="Age (Ma)")
abline(v=66,lty=2) #Maastrichtian
abline(v=56,lty=2) #paleogene
abline(v=33.9,lty=2) #eocene
abline(v=23.03,lty=2) #oligocene
abline(v=20.44,lty=2) #Aquitian
abline(v=15.97,lty=2) #Burdigalian
abline(v=13.82,lty=2) #Langhian
abline(v=11.63,lty=2) #Serravalian
abline(v=7.25,lty=2) #Tortonian
abline(v=5.33,lty=2) #Messinian
abline(v=2.59,lty=2) #Pliocene

###sea levels:
haq<-read.csv("haq_sealevel_curve.csv",head=T)
plot(haq$age,haq$seaLevel,type="l", xlim=c(0,65),ylim=c(-100,220),
xlab="",ylab="Sea Level curve", col="darkviolet")
abline(h=0,lty=2,col="grey")

miller<-read.csv("MillerCurve2005.csv",head=T)
points(miller[,2],miller[,1],type="l", xlim=c(0,65),ylim=c(-100,200),
ylab="",col="red")

muller<-read.csv("MullerCurve2008.csv",head=T)
points(muller[,1],muller[,2],type="l", xlim=c(0,65),ylim=c(-100,400),
xlab="",col="black")
points(muller[,1],muller[,2]-muller[,3],type="l", xlim=c(0,65),
ylab="",col="grey")
points(muller[,1],muller[,2]+muller[,4],type="l", xlim=c(0,65),
ylab="",col="grey")

DeBoer<-read.csv("DeBoer_data.csv",head=T)
points(DeBoer[,1]*-0.001,DeBoer[,2],type="l",ylab="",col="green3") #notice *-0.001 to
standarize scale
```

```

text(31,-18,"Miller",pch=.3,col="red")
text(32,208,"Haq",pch=.3,col="darkviolet")
text(2,101,"Müller",pch=.3)
text(7,-82,"DeBoer",pch=.3,col="green3")

### Temp records
library(zoo)
Beerling<-read.csv("BeerlingTempCO2.csv",head=T)
plot(Beerling$age,Beerling$CO2,type="p",xlim=c(0,65),xlab="",ylab="Atmospheric CO2 (ppm)",
col="black",pch=19)
ma<-rollmean(Beerling$CO2,3,fill = list(NA, NULL, NA))
lines(Beerling$age,ma,col="orange",lwd=2)
abline(h=390, lty=2)
points(DeBoer[,1]*-0.001,DeBoer[,3],type="l",xlim=c(0,65),ylab="",col="blue") #Temp
points(DeBoer[,1]*-0.001,DeBoer[,4],type="l",xlim=c(0,65),ylab="",col="blue") #Deepwater Temp

```

### 9.3.2 - Chapter 5 (Age model):

#### # Fig. 5.2 graphic correlation biplot:

```

## 105 vs SALTARIN
GCSALTARIN_105AM<-read.table("GCSALTARIN_105AM.txt",header=T,sep="\t",na.strings = "NA") #LOC
Salt vs 105
plot(GCSALTARIN_105AM$Saltarin.m,GCSALTARIN_105AM$ X1.AS.105.AM.m, ylab="105-AM (Depths in
m)",
xlab="Saltarin (Depths in m)", ylim=c(380,20),xlim=c(700,0),type="l",col="red")
grid()
events105Saltarin<-read.csv("105AM_Saltarin_events.csv",header=T,na.strings = "NA")
points(events105Saltarin$FADSalt*-1,events105Saltarin$FAD105*-1)
points(events105Saltarin$LADSalt*-1,events105Saltarin$LAD105*-1,pch=4, cex=.7)
#legend
library(gplots)
smartlegend("right","bottom",c("FAD", "LAD","Seq.
strat."),pch=c(1,4,17),inset=0.01,bty="n",cex=.7)

```

#### # Fig. 5.6 Isopach map (kriging):

```

library(maps) #package for basic map
library(mapdata) #package for basic map
library(maptools) #package for basic map

map("worldHires", xlim=c(-75,-60),ylim=c(-12.7,0), border = 0.01,
interior=T,lwd=0.5,lty=4)
box()

```

```

data.s<-read.csv2("para_isopach.csv",header=T)
library(akima) #package to perform Kriging
akima.li <- interp(data.s$x*-1,data.s$y*-1,data.s$z*-1,duplicate="mean")
akima.li.2<-interp(data.s$x*-.1,data.s$y*-.1,data.s$z*-.1,duplicate="mean")

image(akima.li, add=T)

contour(akima.li, nlevels= 20, add=TRUE,lwd=.5)
map("worldHires", xlim=c(-75,-60),ylim=c(-13,0), border = 0.01,
interior=T,lwd=0.5,lty=4,add=T) #repeat map outline

shape <- readShapeLines("lineaire_1km.shp") #shapefile for rivers
plot(shape,add=T,col="grey",lwd=0.4) #rivers

sites2<-read.csv("sites_Acre_Gross.csv",h=T)
points(sites2[1:1,2:3],pch=19,cex=2) #Gross et al 2011 sites
points(sites2[7:16,2:3],pch=19,cex=2) #Latrubesse et al 2010 sites
points(-70.916,-4.383,pch=19,cex=2) #4a
points(-69.933,-4.25,pch=19,cex=2) #105am
points(-67.916,-4.283,pch=19,cex=2) #27am
points(-69.166,-4.55,pch=19,cex=2) #19am
points(-71.4,-4.533,pch=19,cex=2) #32am
points(-63.140833,-4.085,pch=19,cex=2) #Coari
points(-60.077478,-3.117606) #Manaus
points(-73.25,-3.75) #Iquitos
points(-70.63923600, -4.43822400,pch=3,cex=2) #well 2-RC-1 (Miura 1972)
points(-70,-6.5,pch=3,cex=2) #2-EP-1 (approx. location) (Miura 1972)

#adding scale: 1 degree = 111 km//1'=1.85 km//5'=.83 decimals
xe<-c(-74.104,-75)
ye<-c(-12,-12)
lines(xe,ye) #0.896 = 100km
text(-74.5,-12.3,"100 km",cex=.7)

```

### # Fig. 5.7 graphic correlation biplots:

```

## Corr 105 vs 27:
Events105.27<-read.csv("105AM_27AM_events.csv",header=T,na.strings = "NA")
plot(Events105.27$FAD105,Events105.27$FAD27,ylab="27-AM (Depths in m)",
xlab="105-AM (Depths in m)", ylim=c(-390,-30),xlim=c(-380,-20))
points(Events105.27$LAD105,Events105.27$LAD27,pch=4,cex=.7)
grid()

```

```

#legend
library(gplots)
smartlegend("left","top",c("FAD", "LAD"),pch=c(1,4),inset=0.01,bty="n",cex=.7)
text(locator(1),"R. traversei",cex=.7)
text(locator(1),"R. arcus",cex=.7)
text(locator(1),"V. rotundiporus",cex=.7)
text(locator(1),"B. araracuarensis",cex=.7)
text(locator(1),"C. longispinosus",cex=.7)
text(locator(1),"L.? caribbiensis",cex=.7)
text(locator(1),"R. retibolus",cex=.7)
text(locator(1),"B. baculatus",cex=.7)
text(locator(1),"H. incomptus",cex=.7)
text(locator(1),"G. magnaclavata",cex=.7)
text(locator(1),"P. triangularis",cex=.7)

## Corr 105 vs 4a:
Events105.4a<-read.csv("105AM_4aAM_events.csv",header=T,na.strings = "NA")
plot(Events105.4a$FAD105,Events105.4a$FAD4a,ylab="4a-AM (Depths in m)",
xlab="105-AM (Depths in m)", ylim=c(-350,-10),xlim=c(-380,-20))
points(Events105.4a$LAD105,Events105.4a$LAD4a,pch=4,cex=.7)
grid()
#legend
library(gplots)
smartlegend("left","top",c("FAD", "LAD"),pch=c(1,4),inset=0.01,bty="n",cex=.7)
text(locator(1),"B. baculatus",cex=.7)

```

### 9.3.3 - Chapter 6 (Paleoenvironments):

#### # Fig. 6.1 location map with sites from literature:

```

sites<-read.csv("table_map.csv",h=T)
sal_105<-sites[1:2,1:2]
e.m<-sites[3:19,1:2]      #early Miocene sites
em.m<-sites[20:22,1:2]    #early-middle Miocene sites
m.m<-sites[23:37,1:2]     #middle Miocene sites
Mio_indet<-sites[38:54,1:2] #Indet Miocene sites

library(raster) #package to import geotiff file with topography data
library(rgdal) #package to import geotiff file (etopo) with topography data
library(maps) #package to plot basic maps.
library(mapdata) #package to plot basic maps.
library(maptools) #package to plot basic maps.
etopo<-"map.files/ETOPO1_Ice_g_geotiff.tif"

```

```

r.etopo<-raster(etopo)
r.etopo[r.etopo<0]<-NA
r.etopo[r.etopo>600]<-NA

#col=bpy.colors(225)#rainbow, heat.colors, topo.colors, bpy.colors,gray.colors
ext <- extent(-82.5,-58.5,-12,13)

#Map:
zoom(r.etopo, ext=ext,col=rev(gray.colors(225)))
map("worldHires", xlim=c(-82.5,-58.5),ylim=c(-12,13), border = 0.01,
interior =T,lwd=0.5,add=T)
map("rivers", add=T, col="grey50",lwd=0.03)
points(-60.016667,-3.1,pch=3) #Manaus
points(-73.25,-3.733333,pch=3) #Iquitos

points(sal_105,pch=19,cex=0.8)
points(e.m,pch=19,cex=0.8)
points(m.m,pch=15,cex=0.8)
points(em.m,pch=1,cex=0.8)
points(Mio_indet,pch=2,cex=0.8)
numbers<-sites[,13]
text(sites[,1:2]*1.003,labels=c(numbers),cex=.5)

#scale: 1 degree = 111 km//1'=1.85 Km//5'=.83 decimals
xe<-c(-80,-81.792)
ye<-c(-10,-10)
lines(xe,ye) #1.792 = 200km
text(-80.8,-10.5,"200 km",cex=.7)

library(gplots)
smartlegend("right","bottom",
c("Early Miocene","Middle Miocene","Early/Mid. Mioc.,""Undif. Miocene"),
pch=c(19,15,1,2),inset=0.001,bty ="n",cex=.7)

# Fig. 6.2 pollen groups diagrams:

rawdata<-read.csv("Chart_groups.csv",h=T) #counts start in column 8
rawdata[is.na(rawdata)] <- 0 #replace NAs with zeros
data<-cbind(rawdata[3:4],rawdata[6:7],rawdata[9:103]) #gets rid of unimportant columns
(author names, etc)

## Creating objects of sum based on groups:

library(data.table) #for groups sums using data.table()

```



```

DT <- data.table(data)

type<-DT[, lapply(.SD, sum), by = type]
FW<-as.data.frame(type[1,])
FW<-FW[5:99]
MW<-as.data.frame(type[2,])
MW<-MW[5:99]
pollen<-as.data.frame(type[3,])
pollen<-pollen[5:99]
spores<-as.data.frame(type[4,])
spores<-spores[5:99]
#paleoz.acrit<-as.data.frame(type[5,])
#paleoz.acrit<-paleoz.acrit[5:99]
#other.age<-as.data.frame(type[6,])
#other.age<-other.age[5:99]
#cretaceous<-as.data.frame(type[7,])
#cretaceous<-cretaceous[5:99]
#tertiary<-as.data.frame(type[8,])
#tertiary<-tertiary[5:99]
#juras.Cretac.<-as.data.frame(type[9,])
#juras.Cretac.<-juras.Cretac.[5:99]

lifeHabit<-DT[, lapply(.SD, sum), by = life.habit]
tree<-as.data.frame(lifeHabit[3])
tree<-tree[5:99]
herb<-as.data.frame(lifeHabit[4])
herb<-herb[5:99]
RW<-as.data.frame(lifeHabit[8])
RW<-RW[5:99]
unknown<-as.data.frame(lifeHabit[5]) #unknown pollen life habit affinities
unknown<-unknown[5:99]

family<-DT[, lapply(.SD, sum), by = family.subfamily]
poaceae<-as.data.frame(family[40,])
poaceae<-poaceae[5:99]
palms<-as.data.frame(family[9,])
palms<-palms[5:99]
bombac<-as.data.frame(family[31,])
bombac<-bombac[5:99]
sedges<-as.data.frame(family[17,])
sedges<-sedges[5:99]

ecology<-DT[, lapply(.SD, sum), by = ecology]
mangrove<-as.data.frame(ecology[20,])

```

```

mangrove<-mangrove[5:99]
aquaticFern<-as.data.frame(ecology[23,])
aquaticFern<-aquaticFern[5:99]
aquaticHerb<-as.data.frame(ecology[5,])
aquaticHerb<-aquaticHerb[5:99]

other.herb<-herb-poaceae-sedges-aquaticHerb
other.tree<-tree-palms-bombac

## Calculating percentage for each group:
ages<-read.csv("Chart_groups.csv",h=F) #reading excel sheet again w/ h=F (to select ages)
ages<-as.numeric(ages[1,9:103])

groups<-rbind(ages,FW,MW,pollen,spores,tree,herb,poaceae,palms,bombac,
other.herb,other.tree,mangrove,unknown,aquaticFern,aquaticHerb,sedges)

rownames(groups)<-c("ages","FW","MW","pollen","spores","tree","herb",
"poaceae","palms","bombac","other.herb","other.tree","mangrove","unknown",
"aquaticFern","aquaticHerb","sedges")

groups<-as.data.frame(t(groups))
groups<-groups[rowSums(groups[2:5])>100,] #eliminate sums <100

totalSum<-apply(groups[2:5],1,sum) #total sum = algae+dinos+pollen+spores
pollenSum<-apply(groups[4:4],1,sum)
sporesSum<-apply(groups[5:5],1,sum)

FW.P<-groups$FW/totalSum*100
MW.P<-groups$MW/totalSum*100
mangrove.P<-groups$mangrove/pollenSum*100
aquaticHerb.P<-groups$aquaticHerb/pollenSum*100
aquaticFern.P<-groups$aquaticFern/totalSum*100
poaceae.P<-groups$poaceae/pollenSum*100
sedges.P<-groups$sedges/pollenSum*100
palms.P<-groups$palms/pollenSum*100
bombac.P<-groups$bombac/pollenSum*100
other.tree.P<-groups$other.tree/pollenSum*100
other.herb.P<-groups$other.herb/pollenSum*100
spores.P<-groups$spores/totalSum*100
unknown.P<-groups$unknown/pollenSum*100
tree.P<-groups$tree/pollenSum*100

groups.P<-rbind(groups$ages,MW.P,mangrove.P,FW.P,aquaticHerb.P,aquaticFern.P,poaceae.P,

```

```
sedges.P,other.herb.P,palms.P,bombac.P,other.tree.P,spores.P,unknown.P,tree.P) #new groups
using percentages
```

```
rownames(groups.P)<-c("ages","Marine elements","Mangrove pollen","Fresh water algae",
"Aquatic Herbs","Aquatic Ferns","Poaceae","Sedges (Cyperaceae)","Other herbs","Palms",
"Bombacoideae","Other trees","Fern spores","Unknown pollen affinity","Tres total")
```

```
groups.P<-as.data.frame(t(groups.P))
```

```
## Relation Aquatics~Algae:
```

```
aquatics<-aquaticHerb.P+aquaticFern.P
```

```
plot(log(FW.P+1),log(aquatics+1))
```

```
summary(lm(log(FW.P+1)~log(aquatics+1)))
```

```
#Molluscs data for diagram below:
```

```
molluscs<-read.csv("molluscs.csv",h=T)
```

```
molluscs[is.na(molluscs)] <- 0 #replace NAs with zeros
```

```
###Diagram (Fig. 6.2) part 1
```

```
library(rioja) # package that plots diagrams.
```

```
y.tks<-seq(10.7,18.8,0.5)
```

```
depths<-groups.P$ages
```

```
x<-strat.plot (molluscs[2:4],yvar=depths,scale.percent=F,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.05, xRight = .1,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=T, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "Ages(Ma)", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,
  lwd.bar = 4, col.bar = "black", sep.bar = FALSE,
  plot.poly =F,col.poly="blue",col.poly.line="blue",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL, add=T)
```

```
addZone(x,13.72,col="grey50",lty=3) #MM top
```

```
addZone(x,14.15,col="grey50",lty=3) #MM bottom
```

```
addZone(x,17.8,col="grey50",lty=3)#EM top
```

```
addZone(x,18.43,col="grey50",lty=3)#EM bottom
```

```
addZone(x,18.78,col="grey50",lty=2) #FW1 bottom
```

```
addZone(x,15.93,col="grey50",lty=2) #FW2 bottom
```

```

addZone(x,14.97,col="grey50",lty=2) #FW2 top
addZone(x,12.90,col="grey50",lty=2) #FW3 bottom
addZone(x,11.04,col="grey50",lty=2) #FW3 top

par(tcl=-.25)
x<-strat.plot (groups.P[2:3],yvar=depths,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.1, xRight = .21,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=F, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "Ages(Ma)", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,
  lwd.bar = 1, col.bar = "grey", sep.bar = FALSE,
  plot.poly =T,col.poly="blue",col.poly.line="blue",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL, add=T)

```

```

addZone(x,13.72,col="grey50",lty=3) #MM top
addZone(x,14.15,col="grey50",lty=3) #MM bottom
addZone(x,17.8,col="grey50",lty=3)#EM top
addZone(x,18.43,col="grey50",lty=3)#EM bottom
addZone(x,18.78,col="grey50",lty=2) #FW1 bottom
addZone(x,15.93,col="grey50",lty=2) #FW2 bottom
addZone(x,14.97,col="grey50",lty=2) #FW2 top
addZone(x,12.90,col="grey50",lty=2) #FW3 bottom
addZone(x,11.04,col="grey50",lty=2) #FW3 top

```

```

par(tcl=-.25)
x<-strat.plot (groups.P[4:6],yvar=depths,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.20, xRight = .40,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=F, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,
  lwd.bar = 1, col.bar = "grey40", sep.bar = FALSE,
  plot.poly =T,col.poly="turquoise3",col.poly.line="turquoise3",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL, add=T)

```

```

addZone(x,13.72,col="grey50",lty=3) #MM top
addZone(x,14.15,col="grey50",lty=3) #MM bottom
addZone(x,17.8,col="grey50",lty=3)#EM top
addZone(x,18.43,col="grey50",lty=3)#EM bottom
addZone(x,18.78,col="grey50",lty=2) #FW1 bottom
addZone(x,15.93,col="grey50",lty=2) #FW2 bottom
addZone(x,14.97,col="grey50",lty=2) #FW2 top
addZone(x,12.90,col="grey50",lty=2) #FW3 bottom
addZone(x,11.04,col="grey50",lty=2) #FW3 top

par(tcl=-.25)
x<-strat.plot (groups.P[7:9],yvar=depths,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.40, xRight = .60,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=F, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,
  lwd.bar = 1, col.bar = "grey30", sep.bar = FALSE,
  plot.poly =T,col.poly="yellowgreen",col.poly.line="yellowgreen",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL, add=T)

```

```

addZone(x,13.72,col="grey50",lty=3) #MM top
addZone(x,14.15,col="grey50",lty=3) #MM bottom
addZone(x,17.8,col="grey50",lty=3)#EM top
addZone(x,18.43,col="grey50",lty=3)#EM bottom
addZone(x,18.78,col="grey50",lty=2) #FW1 bottom
addZone(x,15.93,col="grey50",lty=2) #FW2 bottom
addZone(x,14.97,col="grey50",lty=2) #FW2 top
addZone(x,12.90,col="grey50",lty=2) #FW3 bottom
addZone(x,11.04,col="grey50",lty=2) #FW3 top

```

```

par(tcl=-.25)
x<-strat.plot (groups.P[10:12],yvar=depths,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.60, xRight = .80,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=F, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,

```

```

lwd.bar = 1, col.bar = "grey", sep.bar = FALSE,
plot.poly = T, col.poly = "darkgreen", col.poly.line = "darkgreen",
lwd.poly = 1, x.names = NULL, cex.xlabel = .88, srt.xlabel = 45,
cex.axis = .8, clust.width = 0.1,
orig.fig = NULL, add = T)

addZone(x, 13.72, col = "grey50", lty = 3) #MM top
addZone(x, 14.15, col = "grey50", lty = 3) #MM bottom
addZone(x, 17.8, col = "grey50", lty = 3) #EM top
addZone(x, 18.43, col = "grey50", lty = 3) #EM bottom
addZone(x, 18.78, col = "grey50", lty = 2) #FW1 bottom
addZone(x, 15.93, col = "grey50", lty = 2) #FW2 bottom
addZone(x, 14.97, col = "grey50", lty = 2) #FW2 top
addZone(x, 12.90, col = "grey50", lty = 2) #FW3 bottom
addZone(x, 11.04, col = "grey50", lty = 2) #FW3 top

par(tcl = -.25)
x <- strat.plot (groups.P[13:13], yvar = depths, scale.percent = T,
  graph.widths = 1, minmax = NULL,
  scale.minmax = F, xLeft = 0.80, xRight = .89,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title = 1.2,
  y.axis = F, min.width = 5, ylim = NULL, y.rev = T,
  y.tks = y.tks, ylabel = "", cex.ylabel = 1, cex.yaxis = .8,
  xSpace = 0.006, wa.order = "none", plot.line = F,
  col.line = "black", lwd.line = 1, plot.bar = T,
  lwd.bar = 1, col.bar = "grey", sep.bar = FALSE,
  plot.poly = T, col.poly = "darkolivegreen", col.poly.line = "darkolivegreen",
  lwd.poly = 1, x.names = NULL, cex.xlabel = .88, srt.xlabel = 45,
  cex.axis = .8, clust.width = 0.1,
  orig.fig = NULL, add = T)

addZone(x, 13.72, col = "grey50", lty = 3) #MM top
addZone(x, 14.15, col = "grey50", lty = 3) #MM bottom
addZone(x, 17.8, col = "grey50", lty = 3) #EM top
addZone(x, 18.43, col = "grey50", lty = 3) #EM bottom
addZone(x, 18.78, col = "grey50", lty = 2) #FW1 bottom
addZone(x, 15.93, col = "grey50", lty = 2) #FW2 bottom
addZone(x, 14.97, col = "grey50", lty = 2) #FW2 top
addZone(x, 12.90, col = "grey50", lty = 2) #FW3 bottom
addZone(x, 11.04, col = "grey50", lty = 2) #FW3 top

par(tcl = -.25)
x <- strat.plot (groups.P[14:14], yvar = depths, scale.percent = T,
  graph.widths = 1, minmax = NULL,

```

```

scale.minmax = F, xLeft = 0.89, xRight = 0.99,
yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
y.axis=F, min.width = 5, ylim = NULL, y.rev = T,
y.tks=y.tks, ylabel = "", cex.ylabel=1, cex.yaxis=.8,
xspace = 0.006, wa.order = "none",plot.line=F,
col.line = "black", lwd.line=1,plot.bar=T,
lwd.bar = 1, col.bar = "black", sep.bar = T,
plot.poly =F,col.poly="",col.poly.line="",
lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
cex.axis=.8, clust.width=0.1,
orig.fig=NULL, add=T)

addZone(x,13.72,col="grey50",lty=3) #MM top
addZone(x,14.15,col="grey50",lty=3) #MM bottom
addZone(x,17.8,col="grey50",lty=3)#EM top
addZone(x,18.43,col="grey50",lty=3)#EM bottom
addZone(x,18.78,col="grey50",lty=2) #FW1 bottom
addZone(x,15.93,col="grey50",lty=2) #FW2 bottom
addZone(x,14.97,col="grey50",lty=2) #FW2 top
addZone(x,12.90,col="grey50",lty=2) #FW3 bottom
addZone(x,11.04,col="grey50",lty=2) #FW3 top

##### Family diagram (individual Families are isolates and a data set is created with them
to build the diagram) – Fig. 6.5.

family<-DT[, lapply(.SD, sum), by = family.subfamily]

Acanthaceae<-as.data.frame(family[2,])
Acanthaceae<-Acanthaceae[5:99]
Alismataceae<-as.data.frame(family[3,])
Alismataceae<-Alismataceae[5:99]
Annonaceae<-as.data.frame(family[4,])
Annonaceae<-Annonaceae[5:99]
Apocynaceae<-as.data.frame(family[4,])
Apocynaceae<-Apocynaceae[5:99]
Aquafoiaceae<-as.data.frame(family[6,])
Aquafoiaceae<-Aquafoiaceae[5:99]
Araliaceae<-as.data.frame(family[7,])
Araliaceae<-Araliaceae[5:99]
Araucariaceae<-as.data.frame(family[8,])
Araucariaceae<-Araucariaceae[5:99]
Arecaceae<-as.data.frame(family[9,])
Arecaceae<-Arecaceae[5:99]

```

```

Asteraceae<-as.data.frame(family[11,])
Asteraceae<-Asteraceae[5:99]
Burseraceae.Sapotaceae<-as.data.frame(family[12,])
Burseraceae.Sapotaceae<-Burseraceae.Sapotaceae[5:99]
Chrysobalanaceae<-as.data.frame(family[13,])
Chrysobalanaceae<-Chrysobalanaceae[5:99]
Cloranthaceae<-as.data.frame(family[14,])
Cloranthaceae<-Cloranthaceae[5:99]
Convolvulaceae<-as.data.frame(family[15,])
Convolvulaceae<-Convolvulaceae[5:99]
Cyperaceae<-as.data.frame(family[17,])
Cyperaceae<-Cyperaceae[5:99]
Ericaceae<-as.data.frame(family[18,])
Ericaceae<-Ericaceae[5:99]
Euphorbiaceae<-as.data.frame(family[19,])
Euphorbiaceae<-Euphorbiaceae[5:99]
Fabaceae.Caesalpinioideae<-as.data.frame(family[20,])
Fabaceae.Caesalpinioideae<-Fabaceae.Caesalpinioideae[5:99]
Fabaceae.Mimosoideae<-as.data.frame(family[21,])
Fabaceae.Mimosoideae<-Fabaceae.Mimosoideae[5:99]
Fabaceae.Papilionoideae<-as.data.frame(family[22,])
Fabaceae.Papilionoideae<-Fabaceae.Papilionoideae[5:99]
Hippocrateaceae<-as.data.frame(family[24,])
Hippocrateaceae<-Hippocrateaceae[5:99]
Humiriaceae<-as.data.frame(family[25,])
Humiriaceae<-Humiriaceae[5:99]
Loranthaceae<-as.data.frame(family[26,])
Loranthaceae<-Loranthaceae[5:99]
Lythraceae<-as.data.frame(family[27,])
Lythraceae<-Lythraceae[5:99]
Malpighiaceae<-as.data.frame(family[28,])
Malpighiaceae<-Malpighiaceae[5:99]
Malvaceae<-as.data.frame(family[29,])
Malvaceae<-Malvaceae[5:99]
Malvaceae.Bombacoideae<-as.data.frame(family[31,])
Malvaceae.Bombacoideae<-Malvaceae.Bombacoideae[5:99]
Malvaceae.Convolvulaceae<-as.data.frame(family[32,])
Malvaceae.Convolvulaceae<-Malvaceae.Convolvulaceae[5:99]
Melastomataceae<-as.data.frame(family[33,])
Melastomataceae<-Melastomataceae[5:99]
Moraceae<-as.data.frame(family[34,])
Moraceae<-Moraceae[5:99]
Myristicaceae<-as.data.frame(family[35,])
Myristicaceae<-Myristicaceae[5:99]

```



```

Myrtaceae<-as.data.frame(family[36,])
Myrtaceae<-Myrtaceae[5:99]
Onagraceae<-as.data.frame(family[37,])
Onagraceae<-Onagraceae[5:99]
Passifloraceae<-as.data.frame(family[38,])
Passifloraceae<-Passifloraceae[5:99]
Pellicieraceae<-as.data.frame(family[39,])
Pellicieraceae<-Pellicieraceae[5:99]
Poaceae<-as.data.frame(family[40,])
Poaceae<-Poaceae[5:99]
Podocarpaceae<-as.data.frame(family[41,])
Podocarpaceae<-Podocarpaceae[5:99]
Polygalaceae<-as.data.frame(family[42,])
Polygalaceae<-Polygalaceae[5:99]
Rhizophoraceae<-as.data.frame(family[43,])
Rhizophoraceae<-Rhizophoraceae[5:99]
Sapindaceae.Proteaceae<-as.data.frame(family[45,])
Sapindaceae.Proteaceae<-Sapindaceae.Proteaceae[5:99]
Sapotaceae<-as.data.frame(family[46,])
Sapotaceae<-Sapotaceae[5:99]
Sapotaceae.Pouteria<-as.data.frame(family[47,])
Sapotaceae.Pouteria<-Sapotaceae.Pouteria[5:99]
Sapotaceae<-Sapotaceae+Sapotaceae.Pouteria
Tiliaceae.Sterculiaceae<-as.data.frame(family[49,])
Tiliaceae.Sterculiaceae<-Tiliaceae.Sterculiaceae[5:99]

## Calculating percentage for each family:
ages<-read.csv("Chart_groups.csv",h=F) #reading excel sheet again w/ h=F (to select ages)
ages<-as.numeric(ages[1,9:103])

groups<-
rbind(pollen,ages,Poaceae,Asteraceae,Ericaceae,Passifloraceae,Convolvulaceae,Cyperaceae,
Alismataceae,Onagraceae,Polygalaceae,Arecaceae,Euphorbiaceae,Melastomataceae,Malvaceae.Bombac
oideae,Rhizophoraceae,Tiliaceae.Sterculiaceae,Araliaceae,Burseraceae.Sapotaceae,Podocarpaceae
,Humiriaceae,Acanthaceae,Annonaceae,Apocynaceae,Aquafoliaceae,Araucariaceae,
Chrysobalanaceae,Cloranthaceae,Fabaceae.Caesalpinioideae,Fabaceae.Mimosoideae,Fabaceae.Papili
onoideae,Hippocrateaceae,Loranthaceae,Lythraceae,Malpighiaceae,Malvaceae,Malvaceae.Convoluta
ceae,Moraceae,Myristicaceae,Myrtaceae,Pellicieraceae,Sapindaceae.Proteaceae,Sapotaceae)

rownames(groups)<-
c("pollen","ages","Poaceae","Asteraceae","Ericaceae","Passifloraceae","Convolvulaceae"
,"Cyperaceae","Alismataceae","Onagraceae","Polygalaceae","Arecaceae","Euphorbiaceae","Melasto
mataceae","Malvaceae.Bombacoideae","Rhizophoraceae","Tiliaceae.Sterculiaceae","Araliaceae","B
urseraceae.Sapotaceae","Podocarpaceae","Humiriaceae","Acanthaceae","Annonaceae","Apocynaceae"

```

```
, "Aquafoliaceae", "Araucariaceae", "Chrysobalanaceae", "Cloranthaceae", "Fabaceae.Caesalpinioidea", "Fabaceae.Mimosoideae", "Fabaceae.Papilionoideae", "Hippocrateaceae", "Loranthaceae", "Lythraceae", "Malpighiaceae", "Malvaceae", "Malvaceae.Convolvulaceae", "Moraceae", "Myristicaceae", "Myrtaceae", "Pellicieraceae", "Sapindaceae.Proteaceae", "Sapotaceae")
```

```
groups<-as.data.frame(t(groups))
groups<-groups[rowSums(groups[3:43])>13,] #eliminate sums <13 (one of lowest numbers of count w/o excluding any family)
depths<-groups$ages
groups<-groups[3:43]/groups$pollen*100
```

```
y.tks<-seq(10.7,18.8,0.5)
```

```
par(tcl=-.25)
x<-strat.plot (groups[1:13],yvar=depths,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.05, xRight = .55,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=TRUE, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "Ages(Ma)", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,
  lwd.bar = 1, col.bar = "grey40", sep.bar = FALSE,
  plot.poly =T,col.poly="darkgreen",col.poly.line="darkgreen",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL)
```

```
par(tcl=-.25)
x<-strat.plot (groups[14:41],yvar=depths,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.55, xRight = .95,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=F, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "Ages(Ma)", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,
  lwd.bar = 1, col.bar = "grey40", sep.bar = FALSE,
  plot.poly =T,col.poly="darkgreen",col.poly.line="darkgreen",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL,add=T)
```

```
#### Dinocysts diagram (Fig. 6.3)

rawdata<-read.csv("dinos.only.csv",h=T) #counts start in column 8
rawdata[is.na(rawdata)] <- 0 #replace NAs with zeros

FW<-as.data.frame(type[1,])
FW<-FW[5:99]
MW<-as.data.frame(type[2,])
MW<-MW[5:99]
pollen<-as.data.frame(type[3,])
pollen<-pollen[5:99]
spores<-as.data.frame(type[4,])
spores<-spores[5:99]

totalSum<-as.numeric(FW+MW+pollen+spores)

aquatic<-rawdata[2:25]/totalSum*100 #2 first FW, rest is MW
aquatic[is.na(aquatic)] <- 0 #replace NAs with zeros
mangrove<-rawdata[26:27]/totalSum*100
mangrove[is.na(mangrove)] <- 0 #replace NAs with zeros
ages<-as.numeric(rawdata$X)

y.tks<-seq(10.7,18.8,0.5)

par(tcl=-.25)
x<-strat.plot (aquatic[1:2],yvar=ages,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.15, xRight = .3,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=T, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "Ages(Ma)", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "bottomleft",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,
  lwd.bar = 1, col.bar = "grey40", sep.bar = FALSE,
  plot.poly =T,col.poly="turquoise3",col.poly.line="turquoise3",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL,add=T)

addZone(x,13.72,col="grey50",lty=3) #MM top
addZone(x,14.15,col="grey50",lty=3) #MM bottom
addZone(x,17.8,col="grey50",lty=3)#EM top
addZone(x,18.43,col="grey50",lty=3)#EM bottom
addZone(x,18.78,col="grey50",lty=2) #FW1 bottom
```

```

addZone(x,15.93,col="grey50",lty=2) #FW2 bottom
addZone(x,14.97,col="grey50",lty=2) #FW2 top
addZone(x,12.90,col="grey50",lty=2) #FW3 bottom
addZone(x,11.04,col="grey50",lty=2) #FW3 top

par(tcl=-.25)
x<-strat.plot (aquatic[3:24],yvar=ages,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.3, xRight = .8,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=F, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "Ages(Ma)", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "bottomleft",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,
  lwd.bar = 1, col.bar = "grey", sep.bar = FALSE,
  plot.poly =T,col.poly="blue",col.poly.line="blue",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL,add=T)

addZone(x,13.72,col="grey50",lty=3) #MM top
addZone(x,14.15,col="grey50",lty=3) #MM bottom
addZone(x,17.8,col="grey50",lty=3)#EM top
addZone(x,18.43,col="grey50",lty=3)#EM bottom
addZone(x,18.78,col="grey50",lty=2) #FW1 bottom
addZone(x,15.93,col="grey50",lty=2) #FW2 bottom
addZone(x,14.97,col="grey50",lty=2) #FW2 top
addZone(x,12.90,col="grey50",lty=2) #FW3 bottom
addZone(x,11.04,col="grey50",lty=2) #FW3 top

par(tcl=-.25)
x<-strat.plot (mangrove,yvar=ages,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.8, xRight = .85,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=F, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "Ages(Ma)", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "bottomleft",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=T,
  lwd.bar = 1, col.bar = "grey", sep.bar = FALSE,
  plot.poly =T,col.poly="darkolivegreen",col.poly.line="darkolivegreen",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL,add=T)

```

```

addZone(x,13.72,col="grey50",lty=3) #MM top
addZone(x,14.15,col="grey50",lty=3) #MM bottom
addZone(x,17.8,col="grey50",lty=3)#EM top
addZone(x,18.43,col="grey50",lty=3)#EM bottom
addZone(x,18.78,col="grey50",lty=2) #FW1 bottom
addZone(x,15.93,col="grey50",lty=2) #FW2 bottom
addZone(x,14.97,col="grey50",lty=2) #FW2 top
addZone(x,12.90,col="grey50",lty=2) #FW3 bottom
addZone(x,11.04,col="grey50",lty=2) #FW3 top

```

**# Boxplots (Fig. 6.4) of %algae and %dinocysts and kruskal/ANOVA tests (results of chapter 6)**  
**of %algae and %dinocysts and %aquatic pollen against lithology:**

```

data<-read.csv("data_divers.csv", head=T)
data[is.na(data)] <- 0
litho<-data[1]
FW<-data[3]
MW<-data[4]
pollenSum<-rowSums(data[5:403])
totalSum<-pollenSum+FW+MW
data2<-cbind(litho,FW/totalSum*100,MW/totalSum*100,pollenSum)
data2<-data2[pollenSum>100,] #eliminate pollen sums <100

par(mfrow=c(1,2))
boxplot(log(FreshwaterAlgae+1)~lithology,data=data2,
ylab="log % Freshwater algae")

shapiro.test(data2$FreshwaterAlgae) #not normal, thus a kruskal-wallis will be used
kruskal.test(FreshwaterAlgae~lithology,data=data2)

library(PMCMR) #to run KW post hoc Tukey test
posthoc.kruskal.nemenyi.test(FreshwaterAlgae~lithology,data=data2,dist="Tukey")

boxplot(log(Dinocysts+1)~lithology,data=data2,ylab="log % Dinocysts")
shapiro.test(data2$Dinocysts) #not normal, thus a kruskal-wallis will be used
kruskal.test(Dinocysts~lithology,data=data2) #there are no sig. differences

text(2.572,3.917,"MF1 and MF2
Dinocyst spikes", cex=.8)

##Aquatic vs Litho:

```

```

data<-read.csv("Aquatic_vs_litho.csv", head=T)
data[is.na(data)] <- 0

litho<-data[1]
aquatic<-data[3]
FW<-data[4]
MW<-data[5]
pollenSum<-rowSums(data[6:404])
totalSum<-pollenSum+FW+MW

data2<-cbind(litho,aquatic/totalSum*100,pollenSum)
data2<-data2[pollenSum>100,] #eliminate pollen sums <100

boxplot(log(totalAquatic+1)~lithology,data=data2,
ylab="log % Fresh water algae")

shapiro.test(data2$totalAquatic) #normal
aov<-aov(totalAquatic~lithology,data=data2)
summary(aov)

```

#### **# Canonical Correspondence Analysis (Table 6.1) location map with sites from literature:**

```

data<-read.csv("Chart_CCA.csv",h=T)
data[is.na(data)]<-0
data<-data[rowSums(data[9:410])>100,]
data<-data[,colSums(data)>3]

environ<-data[1:8] #environmental variables
veg<-log(data[9:178]+1) #vegetation matrix

library(vegan)
cca.1<-cca(veg~Freshwater+PeakMarine,data=environ) #runs cca
cca.1 #CCA summary

#cca w binary data set:
veg<-data[9:178]
veg<-ifelse(veg[, -1]>=1,1,0) #transforming data into binary

cca.1<-cca(veg~Freshwater+PeakMarine,data=environ) #runs cca
cca.1 #CCA summary

```

**# Diagram (Fig. 6.6) of marine-freshwater elements from Saltarin and 105-am, plus sea level**

**curves:**

**##Saltarin:**

```
rawdata<-read.csv("DataSaltarin.csv",h=T)
rawdata[is.na(rawdata)] <- 0
data<-rawdata[rowSums(rawdata[8])>100,] #eliminate sums <100
FWperc<-data$FW/data$Total.Sum*100
Marine<-(data$Dinos+data$Foram.lining)/data$Total.Sum*100
groups.P<-cbind(data$age, FWperc, Marine)
groups.P<-as.data.frame(groups.P[21:96,]) #excl. Late Mioc samples
```

**###Diagrama parte 1**

```
library(rioja) #package that plots diagram
```

```
y.tks<-seq(10.7,18.7,0.5)
```

```
depths<-groups.P[,1]
```

```
par(tcl=-.25)
```

```
x<-strat.plot (groups.P[2:3],yvar=depths,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.1, xRight = .51,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=TRUE, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "Ages(Ma)", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=F,
  lwd.bar = 1, col.bar = "grey", sep.bar = FALSE,
  plot.poly =T,col.poly=c("turquoise3","blue"),col.poly.line=c("turquoise3","blue"),
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL, add=T)
```

```
addZone(x,13.72,col="grey50",lty=3) #MM top
```

```
addZone(x,14.15,col="grey50",lty=3) #MM bottom
```

```
addZone(x,17.8,col="grey50",lty=3)#EM top
```

```
addZone(x,18.43,col="grey50",lty=3)#EM bottom
```

**##105-AM:**

```
rawdata<-read.csv("FWMW_105.csv",h=T)
rawdata[is.na(rawdata)] <- 0
data<-rawdata[rowSums(rawdata[6])>100,] #eliminate sums <100

FWperc<-data$FW/data$TotalSum*100
Marine<-(data$Dinocysts+data$Forams)/data$TotalSum*100
```

```

groups.P<-cbind(data$age, Fwperc, Marine)

y.tks<-seq(10.7,18.7,0.5)
depths<-groups.P[,1]

par(tcl=-.25)
x<-strat.plot (groups.P[,2:3],yvar=depths,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.6, xRight = .95,
  yBottom = 0.045, yTop = 0.85, title = "", cex.title=1.2,
  y.axis=TRUE, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "", cex.ylabel=1, cex.yaxis=.8,
  xSpace = 0.006, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=F,
  lwd.bar = 1, col.bar = "grey", sep.bar = FALSE,
  plot.poly =T,col.poly=c("turquoise3","blue"),col.poly.line=c("turquoise3","blue"),
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL, add=T)

addZone(x,13.72,col="grey50",lty=3) #MM top
addZone(x,14.15,col="grey50",lty=3) #MM bottom
addZone(x,17.8,col="grey50",lty=3)#EM top
addZone(x,18.43,col="grey50",lty=3)#EM bottom

###sea levels:
haq<-read.csv("haq_sealevel_curve.csv",head=T)
par(mfrow=c(1,2))
plot(haq$seaLevel,haq$age,type="l", ylim=c(18.7,10.7),xlim=c(-80,160),
xlab="Sea Level curve",ylab="Age (Ma)", col="grey",lty=2,lwd=2)

miller<-read.csv("MillerCurve2005.csv",head=T)
points(miller[,1],miller[,2],type="l", ylim=c(18.7,10.7),xlim=c(-80,160),
ylab="",col="grey",lwd=2)

muller<-read.csv("MullerCurve2008.csv",head=T)
#points(muller[,2],muller[,1],type="l", ylim=c(18.7,10.7),xlim=c(-80,160),
xlab="",col="black")
#points(muller[,2]-muller[,3],muller[,1],type="l", xlim=c(0,65),
ylab="",col="grey")
#points(muller[,2]+muller[,4],muller[,1],type="l", xlim=c(0,65),
ylab="",col="grey")

DeBoer<-read.csv("DeBoer_data.csv",head=T)

```



```

points(DeBoer[,2],DeBoer[,1]*-0.001,type="l",ylab="",col="black",lwd=2) #notice *-0.001 to
standardize scale
abline(v=0,lty=2)
text(31,-18,"Miller",pch=.3,col="red")
text(32,208,"Haq",pch=.3,col="darkviolet")
text(2,101,"Müller",pch=.3)
text(7,-82,"DeBoer",pch=.3,col="green3")

##Zachos
data<-read.csv("zachos2008.csv",head=T)
plot(data$d18O.5pt,data$Age,ylim=c(18.7,10.7), xlim=c(3,1.3),type="l",col="blue",lwd=1.5,
xlab="d18O",ylab="")
#plot(data$d13C.5pt,data$Age,ylim=c(18.7,10.7),type="l",col="green4",lwd=1.5,
ylab="d13C",xlab="Age (Ma)")
abline(h=18.7)
abline(h=10.7)

```

### 9.3.4 - Chapter 7 (Diversity). Codes for figures and analyses.

**# preparing the data plus Fig. 7.1 (abundance and evenness distribution over ages):**

```

data<-read.csv("data_divers.csv", h=T)
data300<-data[1:405] #selects pollen+spores counts only
data300[is.na(data300)] <- 0 #replace NAs with zeros
data300.sum<-apply(data300[3:405], 1, sum) #row sums

plot(data300.sum,data300[,2],ylim=c(19,10), ylab="Age (ma)",
xlab="Pollen count, cutoff=226")
abline(v=223,lty=2)

data226<-data300[rowSums(data300[3:405])>225,] #excludes rows < 226 count. Note first column
(ages) is not included in the row sum
data226.sum<-apply(data226[3:405], 1, sum) #new row sums
points(data226.sum,data226[,2],ylim=c(19,10.5),cex=.5, col="red") #plotting to confirm subset
was correctly made

#At this point, a new dataset has been produced with pollen counts >= 226. Now, some
diversity metrics will be calculated including evenness, after that a new dataset will be
produced excluding samples with very low evenness:

library(vegan)
ages<-data226[,2]
raremin<-min(rowSums(data226[3:405])) #shows lowest count, which I know already from the
routine (and plot) above
H<-diversity(data226[3:405],index="shannon") #shannon index

```

```

S<-specnumber(data226[3:405]) #number of species (richness)
J<-H/log(S) #evenness

plot(J, ages,ylim=c(19,10),type="b",xlab="evenness",ylab="ages (ma)") #plotting evenness vs
age:
abline(v=0.405,lty=2)
points(J[25],ages[25],pch=20)
points(J[57],ages[57],pch=20)
points(J[64],ages[64],pch=20)

data226$J<-J #adds "J" column of evenness values to data.frame (which is now 405 columns long)
data226<-data226[data226["J"]>0.4,] #excludes rows < 0.4 evenness (3 samples)

##### New diversity indexes and evenness
ages<-data226[,2]
Srare<-rarefy(data226[3:405], 226)
H<-diversity(data226[3:405],index="shannon") #shannon index
S<-specnumber(data226[3:405]) #number of species (richness)
J<-H/log(S) #evenness

plot(J, ages,ylim=c(19,10),type="b",xlab="evenness",ylab="ages (ma)") #plotting evenness vs
age:
abline(v=0.405,lty=2)
mean(J[1:36])
mean(J[37:67])
wilcox.test(J[1:37],J[38:70])
text(0.77,13.3,"mean=0.66",cex=.8)
text(0.77,17.3,"mean=0.63",cex=.8)
legend("topleft","p-value=0.09",cex=.8,box.lty=0)
abline(v=0.66)
abline(v=0.63)

##### Rarefied diversity (Fig. 7.2-a)
plot(Srare,ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="Rarefied diversity")
points(Srare[1:36],ages[1:36],pch=20)
mean(Srare[1:36])
mean(Srare[37:67])
wilcox.test(Srare[1:37],Srare[38:70])
text(50.5,13.4,"mean=36.7",cex=.8)
text(50.5,17.3,"mean=25",cex=.8)
legend("topleft","p-value=1.966e-06",cex=.8,box.lty=0)
abline(v=36.7)
abline(v=25)

```

#### #####Diversity Shannon (Fig. 7.2-b)

```
plot(H,ages,ylim=c(19,10),type="b",ylab="Age (ma)",xlab="H' diversity")
points(H[1:37],ages[1:37],pch=20)
```

```
mean(H[1:36]) #2.4
mean(H[37:67]) #2.0
text(3,13,"mean=2.4",cex=.8)
text(3,17,"mean=2.0",cex=.8)
abline(v=2.4)
abline(v=2.0)
```

```
wilcox.test(H[1:37],H[38:70]) #p-value=0.0003596
legend("topleft", "p-value=0.0003596",cex=.8,box.lty=0)
```

#### ##### DCA (Table 7.1 and Fig. 7.2-c and d)

```
dataDCA<-log(data226[3:405]+1)
#dataDCA<-log(data226[,colSums(data226[3:405])>1]+1) #exlc. singletons
DCA<-decorana(dataDCA,iweigh=1)
axis1<-DCA$rproj[,1]
axis2<-DCA$rproj[,2]
```

```
plot(DCA, display="none",xlim=c(0,2.5),ylim=c(0,2.5))
points(axis1[1:37],axis2[1:37],xlim=c(0,2.5),ylim=c(0,3),pch=20)
points(axis1[38:70],axis2[38:70],xlim=c(0,2.5),ylim=c(0,3))
text(0.31,1.33,"pos-16Ma",cex=.8)
text(1.7,1.06,"pre-16Ma",cex=.8)
text(1.6,2.4,"Bottom 3 samples",cex=.8)
```

```
mean(axis1[1:36])
mean(axis1[37:67])
wilcox.test(axis1[1:36],axis1[37:67])
```

```
plot(axis1, ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",xlab="DCA axis 1")
text(1,12.70,"mean=0.35",cex=.8)
text(1.8,17,"mean=1.24",cex=.8)
text(2,10,"p-value=2.2e-16",cex=.8)
abline(v=0.35)
abline(v=1.24)
points(axis1[1:36], ages[1:36],pch=20)
```

```
mean(axis2[1:36])
mean(axis2[37:67])
wilcox.test(axis2[1:36],axis2[37:67])
```

```

plot(axis2, ages,ylim=c(19.5,10),type="b",ylab="",xlab="DCA axis 2")
points(axis2[1:37], ages[1:37],pch=20)
text(1.9,13.4,"mean=0.83",cex=.8)
text(1.9,17.36,"mean=0.90",cex=.8)
text(2.2,10,"p-value=0.5696",cex=.8)
abline(v=0.83)
abline(v=0.90)

```

#### ##### Lithology (data preparation, boxplots and analyses) (Fig. 7.3 and 7.4)

```

younger<-rep("younger",35)
older<-rep("older",32)
strata<-matrix(c(rep("younger",35),rep("older",32)))

litho.data<-data.frame(data226[2:2],data226[1:1],Srare,axis1,axis2,H,J,strata)

library(plyr)
count(litho.data$lithology) #counts how many samples per lithology

par(mfrow=c(3,2))
boxplot(litho.data$Srare~litho.data$lithology,ylab="Rarefied diversity",
main="n=12          n=29          n=10          n=16")
boxplot(litho.data$H~litho.data$lithology,ylab="H' diversity")
boxplot(litho.data$axis1~litho.data$lithology,ylab="DCA axis 1")
boxplot(litho.data$axis2~litho.data$lithology,ylab="DCA axis 2")
boxplot(litho.data$J~litho.data$lithology,ylab="Eveness")

plot(litho.data$Srare,litho.data$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="Rarefied diversity")
points(litho.data$Srare,litho.data$ages,col=litho.data$lithology,pch=20)
legend('topleft',legend=levels(litho.data$lithology),col=1:4,cex=0.8,pch=20)
abline(h=17.8,lty=2)
abline(h=18.03,lty=2)
abline(h=14.09,lty=2)
abline(h=13.73,lty=2)

plot(litho.data$axis1,litho.data$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="DCA axis 1")
points(litho.data$axis1,litho.data$ages,col=litho.data$lithology,pch=20)
legend('topright',legend=levels(litho.data$lithology),col=1:4,cex=0.8,pch=20)

plot(litho.data$axis2,litho.data$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="DCA axis 2")
points(litho.data$axis2,litho.data$ages,col=litho.data$lithology,pch=20)

```

```
legend('topright',legend=levels(litho.data$lithology),col=1:4,cex=0.8,pch=20)
```

**### ANOVA diversity metrics vs lithologies (results of a post-hoc Tukey test is at the end of this appendix):**

#shapiro.test() = The null hypothesis for this test is that the data are normally distributed. The Prob < w value listed in the output is the p-value. If the chosen alpha level is 0.05 and the p-value is less than 0.05, then the null hypothesis that the data are normally distributed is rejected. If the p-value is greater than 0.05, then the null hypothesis is not rejected.

```
shapiro.test(sqrt(litho.data$Srare))    #p=0.1429 sqrt-ed to meet ANOVA assumptions
shapiro.test(litho.data$H)             #p=0.9738
shapiro.test(litho.data$J)             #p=0.3017
shapiro.test(sqrt(litho.data$axis1))    #p=0.2341 sqrt-ed to meet ANOVA assumptions
```

```
aov<-aov(sqrt(Srare)~lithology*strata, data=litho.data)
summary(aov)
print(model.tables(aov,"means",digit=3))
TukeyHSD(aov,order=T)
shapiro.test(aov$residuals)    #p=0.2423
```

```
aov<-aov(H~lithology*strata, data=litho.data)
summary(aov)
print(model.tables(aov,"means",digit=3))
TukeyHSD(aov,order=T)
shapiro.test(aov$residuals)    #p=0.8008
```

```
aov<-aov(J~lithology*strata, data=litho.data)
summary(aov)
print(model.tables(aov,"means",digit=3))
TukeyHSD(aov,order=T)
shapiro.test(aov$residuals)    #p=0.3137
```

```
aov<-aov(sqrt(axis1)~lithology*strata, data=litho.data)
summary(aov)
print(model.tables(aov,"means",digit=3))
TukeyHSD(aov,order=T)
shapiro.test(aov$residuals)    #p=0.04856
```

**#####creates subsets by lithology:**

```
mudstone<-subset(litho.data,lithology=="mudstone")
siltstone<-subset(litho.data,lithology=="siltstone")
sandstone<-subset(litho.data,lithology=="sandstone")
lignite<-subset(litho.data,lithology=="lignite")
```

```

fines<-rbind(mudstone,lignite)    #creates data.frame w muds and lignites
fines<-fines[order(fines$ages),]  #orders by ages

plot(fines$Srare,fines$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="Rarefied diversity", main="Mudstones+lignites")
points(fines$Srare,fines$ages,col=fines$lithology,pch=20)
text(18,10,"p-value=0.003013",cex=.8)
wilcox.test(fines$Srare[1:17],fines$Srare[18:41])

plot(fines$H,fines$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="H diversity", main="Mudstones+lignites")
points(fines$H,fines$ages,col=fines$lithology,pch=20)
text(1.46,10,"p-value=0.02787",cex=.8)
wilcox.test(fines$H[1:17],fines$H[18:41])

plot(fines$axis1,fines$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="DCA axis 1", main="Mudstones+lignites")
points(fines$axis1,fines$ages,col=fines$lithology,pch=20)
text(2,10,"p-value=3.589e-09",cex=.8)
wilcox.test(fines$axis1[1:17],fines$axis1[18:41])

#testing differences of mudstones only:
wilcox.test(mudstone$Srare[1:16],mudstone$Srare[17:29]) #p-value = 0.0196
wilcox.test(mudstone$axis1[1:16],mudstone$axis1[17:29]) #p-value = 8.841e-07
wilcox.test(mudstone$H[1:16],mudstone$H[17:29])          #p-value = 0.09161

siltsand<-rbind(siltstone,sandstone)    #creates data.frame w silts and sandss
siltsand<-siltsand[order(siltsand$ages),]  #orders by ages

plot(siltsand$Srare,siltsand$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="Rarefied diversity", main="Silts+Sands")
points(siltsand$Srare,siltsand$ages,col=siltsand$lithology,pch=20)
text(23,10,"p-value=0.05397",cex=.8)
text(23,10.6,"p-value=7.905e-05
(excl.bottom sample)",cex=.8)
wilcox.test(siltsand$Srare[1:19],siltsand$Srare[20:26])

plot(siltsand$H,siltsand$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="H diversity", main="Silts+Sands")
points(siltsand$H,siltsand$ages,col=siltsand$lithology,pch=20)
text(1.86,10,"p-value=0.02547",cex=.8)
text(1.87,10.6,"p-value=0.001016
(excl.bottom sample)",cex=.8)

```

```

wilcox.test(siltsand$H[1:19],siltsand$H[20:26])

plot(siltsand$axis1,siltsand$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="DCA axis 1", main="Silts+Sands")
points(siltsand$axis1,siltsand$ages,col=siltsand$lithology,pch=20)
text(.15,10,"p-value=6.081e-06",cex=.8)
wilcox.test(siltsand$axis1[1:19],siltsand$axis1[20:26])

exclign<-rbind(siltstone,sandstone,mudstone) #creates data.frame excl. lignites
exclign<-exclign[order(exclign$ages),]      #orders by ages

plot(exclign$Srare,exclign$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="Rarefied diversity", main="All except lignites")
points(exclign$Srare,exclign$ages,col=exclign$lithology,pch=20)
text(19,10,"p-value=2.071e-05",cex=.8)
text(19,10.6,"p-value=1.588-e06
(excl.bottom sample)",cex=.8)
wilcox.test(exclign$Srare[1:35],exclign$Srare[36:55])
abline(v=mean(exclign$Srare[1:35]))
abline(v=mean(exclign$Srare[36:55]))

plot(exclign$H,exclign$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="H diversity", main="All except lignites")
points(exclign$H,exclign$ages,col=exclign$lithology,pch=20)
text(1.5,10,"p-value=0.0009952",cex=.8)
text(1.5,10.6,"p-value=0.0001555
(excl.bottom sample)",cex=.8)
wilcox.test(exclign$H[1:35],exclign$H[36:55])
abline(v=mean(exclign$H[1:35]))
abline(v=mean(exclign$H[36:55]))

plot(exclign$axis1,exclign$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="DCA axis 1", main="All except lignites")
points(exclign$axis1,exclign$ages,col=exclign$lithology,pch=20)
text(.15,10,"p-value=1.077e-12",cex=.8)
wilcox.test(exclign$axis1[1:35],exclign$axis1[36:55])
abline(v=mean(exclign$axis1[1:35]))
abline(v=mean(exclign$axis1[36:55]))

MUDsilt<-rbind(siltstone,mudstone)          #creates data.frame w muds and silts
MUDsilt<-MUDsilt[order(MUDsilt$ages),]      #orders by ages

plot(MUDsilt$Srare,MUDsilt$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="Rarefied diversity", main="Muds+Silts")

```

```

points(MUDsilt$Srare,MUDsilt$ages,col=MUDsilt$lithology,pch=20)
text(19,10,"p-value=0.0003695",cex=.8)
text(19,10.6,"p-value=5.436e-05
(excl.bottom sample)",cex=.8)
wilcox.test(MUDsilt$Srare[1:26],MUDsilt$Srare[27:45])
abline(v=mean(MUDsilt$Srare[1:26]))
abline(v=mean(MUDsilt$Srare[27:45]))

plot(MUDsilt$H,MUDsilt$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="H diversity", main="Muds+Silts")
points(MUDsilt$H,MUDsilt$ages,col=MUDsilt$lithology,pch=20)
text(1.5,10,"p-value=0.01083",cex=.8)
text(1.5,10.6,"p-value=0.002785
(excl.bottom sample)",cex=.8)
wilcox.test(MUDsilt$H[1:26],MUDsilt$H[27:45])
abline(v=mean(MUDsilt$H[1:26]))
abline(v=mean(MUDsilt$H[27:45]))

plot(MUDsilt$axis1,MUDsilt$ages,ylim=c(19.5,10),type="b",ylab="ages (Ma)",
xlab="DCA axis 1", main="Muds+Silts")
points(MUDsilt$axis1,MUDsilt$ages,col=MUDsilt$lithology,pch=20)
text(.15,10,"p-value=2.231e-10",cex=.8)
wilcox.test(MUDsilt$axis1[1:26],MUDsilt$axis1[27:45])
abline(v=mean(MUDsilt$axis1[1:26]))
abline(v=mean(MUDsilt$axis1[27:45]))

```

#### ##### Among sample Diversity (Fig. 7.5-a and difference tests):

#two groups:

```

spk<-specaccum(data226[1:36,3:405],ci=1,method="rarefaction")
spk2<-specaccum(data226[37:67,3:405],ci=1,method="rarefaction")

```

```

par(mfrow=c(1,3))
plot(spk,ylab="Number of species", xlab="Number of pooled samples",ci.lty=2,
ci.type="line",lwd=1.5,ylim=c(45,300))
plot(spk2,ylab="Number of species", xlab="Number of pooled samples",ci.lty=2,
ci.type="line",lwd=1.5,col="grey",ci.col="grey",add=T)

```

```

wilcox.test(spk$richness[1:31], spk2$richness) #at 31 samples
text(17.4, 258,"post-16Ma",cex=.8)
text(23.8,167,"pre-16Ma",cex=.8,col="grey40")
text(4.25,300,"p-value=0.01249",cex=.8)

```

#### #among sample divers. using Chao2 and Jackknife2 (Fig. 7.5-b and c, and difference tests)



```

Chao2.estimateds<-poolaccum(data226[1:36,3:405],permutations=1000)#calc. diversities estimates
Chao2.estimateds<-summary(Chao2.estimateds,display="chao") #selects chao2
Chao2.estimateds2<-poolaccum(data226[37:67,3:405],permutations=1000)
Chao2.estimateds2<-summary(Chao2.estimateds2,display="chao")

```

```

plot(Chao2.estimateds[[1]][,1],Chao2.estimateds[[1]][,2],type="l",xlim=c(0,40),ylim=c(0,700)
,ylab="Number of pooled samples",ylab ="Chao2 estimated species richness")
lines(Chao2.estimateds[[1]][,1],Chao2.estimateds[[1]][,3], lty = 2)
lines(Chao2.estimateds[[1]][,1],Chao2.estimateds[[1]][,4], lty = 2)

```

```

lines(Chao2.estimateds2[[1]][,1],Chao2.estimateds2[[1]][,2],type="l",col ="grey",add=T)
lines(Chao2.estimateds2[[1]][,1],Chao2.estimateds2[[1]][,3], lty = 2, col="grey")
lines(Chao2.estimateds2[[1]][,1],Chao2.estimateds2[[1]][,4], lty = 2, col="grey")
text(3.5,700,"p-value=0.2651",cex=.8)
wilcox.test(Chao2.estimateds[[1]][1:29,2],Chao2.estimateds2[[1]][,2])

```

```

Jack2.estimateds<-poolaccum(data226[1:36,3:405],permutations=1000) #calc.diversities estimates
Jack2.estimateds<-summary(Jack2.estimateds,display="jack2") #selects chao2
Jack2.estimateds2<-poolaccum(data226[37:67,3:404],permutations=1000)
Jack2.estimateds2<-summary(Jack2.estimateds2,display="jack2")

```

```

plot(Jack2.estimateds[[1]][,1],Jack2.estimateds[[1]][,2],type="l",xlim=c(0,40),ylim=c(0,550)
,ylab="Number of pooled samples",ylab ="Jackknife2 estimated species richness")
lines(Jack2.estimateds[[1]][,1], Jack2.estimateds[[1]][,3], lty = 2)
lines(Jack2.estimateds[[1]][,1],Jack2.estimateds[[1]][,4], lty = 2)

```

```

lines(Jack2.estimateds2[[1]][,1],Jack2.estimateds2[[1]][,2],type="l",col ="grey",add=T)
lines(Jack2.estimateds2[[1]][,1],Jack2.estimateds2[[1]][,3], lty = 2, col="grey")
lines(Jack2.estimateds2[[1]][,1],Jack2.estimateds2[[1]][,4], lty = 2, col="grey")
text(3.2,555,"p-value=0.06392",cex=.8)
wilcox.test(Jack2.estimateds[[1]][1:29,2],Jack2.estimateds2[[1]][,2])

```

#### **#amount of singletons pre and post-16**

```

full<-data226[3:405]
full<-full[,colSums(full)==1]
SumPOS16<-colSums(full[1:36,])
sum(SumPOS16) #92 taxa
SumPRE16<-colSums(full[37:67,])
sum(SumPRE16) #51 taxa

```

#### **##### Piecewise regression and Fig. 7.6-a:**

```

#cumulative FAD-LAD plot:
data<-data[2:91,] #excludes topmost and bottommost samples (where FAD-LAD accumulates
disproportionally)

```

```

data<-data[,colSums(data)>1] #exclue singletons (it is now 90x231)
counts<-data[2:231]
depths<-data$age
sample.labels<-data$age
edge=strat.column(counts=counts,depths=depths,sample.labels=sample.labels)

FAD=fads(edge,increasing.down=T)#FAD, singles excluded
LAD=lads(edge,increasing.down=T)#LAD, singles excluded

plot(rev(sort(FAD)), ylim=c(19,10), ylab="Age(Ma)",xlab="Cumulative FAD/LAD")
points(rev(sort(LAD)),pch=19) #used rev() to make plot similar to range chart
legend("topleft",legend=c("FAD","LAD"),pch=c(1,19),box.lty=0,cex=.8)
abline(h=18.24,lty=2) #fad.edge[breakpoint]
abline(h=11.25,lty=2) #lad.edge[breakpoint]
,decreasing=T

###Piecewise regression (codes from Jaramillo et al. 2006, 2010)

(max(depths)+min(depths))/2 #age central point=14.805

##FAD EDGE
fad.edge<-FAD[which(FAD>14.8)]##time restricted to edge effect for FAD
fad.edge<-sort(fad.edge,decreasing=T)##fad arranged from oldest to youngest
span=length(fad.edge)#length of the analysis, to be included in the next line
cumuedge.fad<-c(1:span)
step1<-numeric(span)##first segment of piecewise
for (i in (1:span)){
step1[i]<-sum(resid(lm(fad.edge[1:i]~cumuedge.fad[1:i]))^2)
}
step2<-numeric(span)##last segment of piecewise
for (i in (1:span)){
step2[i]<-sum(resid(lm(fad.edge[i:span]~cumuedge.fad[i:span]))^2)
}
piecewise<-step1+step2## sum of first and second segment
breakpoint=which(piecewise==min(piecewise))## the position of the minimum value
fad.edge[breakpoint]##18.24 Ma

##LAD EDGE
lad.edge<-LAD[which(LAD<14.8)]##time restricted to edge effect for FAD
lad.edge<-sort(lad.edge)##lad arranged from youngest to oldest
span=length(lad.edge)#length of the analysis, to be included in the next line
cumuedge.lad<-c(1:span)
step1<-numeric(span)##first segment of piecewise
for (i in (1:span)){

```

```

step1[i]<-sum(resid(lm(lad.edge[1:i]~cumuedge.lad[1:i]))^2)
}
step2<-numeric(span)##last segment of piecewise
for (i in (1:span)){
step2[i]<-sum(resid(lm(lad.edge[i:span]~cumuedge.lad[i:span]))^2)
}
piecewise<-step1+step2## sum of first and second segment
breakpoint=which(piecewise==min(piecewise))## the position of the minimum value
lad.edge[breakpoint]##11.25

##### Originations and extinction rates and standing diversity (Fig. 7.6-b and c)
data.oe<-data300[3:404]
ages.oe<-as.character(data300["ages"])
ages.oe<-data300$ages

library(stratigraph)
oe<-oe.rates(data.oe, depths = NULL, breaks = NULL,
per.capita = T, remove.below = 2) #function that calculates standing diversity, origination
#and extinction
divers<-oe$basic[,1] #isolates standing diversity
origin<-oe$basic[,2] #isolates origination
extinc<-oe$basic[,3] #isolates extinction

plot(divers,ages.oe,pch=20, ylim=c(19.5,10),xlim=c(60,170),
ylab="Age (Ma)",xlab="Standing diversity")
abline(h=18.24,lty=2) #fad.edge[breakpoint]
abline(h=11.25,lty=2) #lad.edge[breakpoint]

plot(origin,ages.oe,pch=20, ylim=c(19.5,10),xlim=c(0,0.2),
ylab="Age (Ma)",xlab="per-capita rates")
points(extinc,ages.oe, ylim=c(19.5,10),ylab="Age (Ma)",col="gray50")
abline(v=0)
library(gplots)
smartlegend("right","top",c("Origination", "Extinction"),pch=c(20,1),inset=0.001,
bty = "n",cex=.8)
abline(h=18.24,lty=2) #fad.edge[breakpoint]
abline(h=11.25,lty=2) #lad.edge[breakpoint]

# Origin~extinc (Fig. 7.8)
#First, run oe.rates(...per.capita=F). Second, excl. samples below/above edge effect (8
bottom samples + 5 top samples = from sample 6 to sample 71)

plot(log(origin[6:71]+1), log(extinc[6:71]+1), xlab="Log Originations", ylab="Log
Extinctions")

```

```

x<-lm(log(extinc[6:71]+1)~ log(origin[6:71]+1))
abline(x)
rs<-expression(paste(r^2 ,"=0.35", sep = ""))
p<-"p<0.000001"
smartlegend("left","top",c(rs,
p),inset=0,bty ="n",cex=.85)

```

### ### Time Series Analysis (Table 7.3):

```

bin.dataTS<-data.frame(ages,Srare,axis1,axis2,H) #creates dataframe with ages, originations
and extinctions
bin.dataTS$bin<-cut(bin.dataTS$ages,breaks=seq(10.72,18.75,by=0.5),labels=1:16,
include.lowest=T) #adds a 'bin' variable to the dataframe above, bins every 0.5 Ma
bin.dataTS[67,"bin"]<-16 #replacing last bin number which was NA for a 16

```

```

library(plyr) #to use ddply() in order to calculate means

```

```

#calculates means for each variable based on factor bin:

```

```

bin.meansTS<-ddply(bin.dataTS,.(bin), function(x) data.frame(ages=mean(x$ages),
Srare=mean(x$Srare),axis1=mean(x$axis1),axis2=mean(x$axis2),H=mean(x$H)))

```

```

#calculates sd for each variable based on factor bin

```

```

bin.sdTS<-ddply(bin.dataTS,.(bin), function(x) data.frame(ages=sd(x$ages),
Srare=sd(x$Srare),axis1=sd(x$axis1),axis2=sd(x$axis2),H=sd(x$H)))

```

```

#preparing data.frame for PaleoTS() run (on rar. diversity):

```

```

fullsize<-c(4,3,4,4,3,3,2,2,4,3,8,5,5,5,4,8)
fullmean<-bin.meansTS$Srare
fullvar<-bin.sdTS$Srare
age<-bin.meansTS$ages
dataTS<-data.frame(fullsize,fullmean,fullvar,age)

```

```

library(paleoTS)

```

```

PALEO.data<-as.paleoTS(mm=dataTS$fullmean,vv=dataTS$fullvar,
nn=dataTS$fullsize,tt=dataTS$age)
x<-fit3models(PALEO.data)

```

```

#preparing data.frame for PaleoTS() run (on H' diversity):

```

```

fullmean<-bin.meansTS$H
fullvar<-bin.sdTS$H
dataTS<-data.frame(fullsize,fullmean,fullvar,age)
PALEO.data<-as.paleoTS(mm=dataTS$fullmean,vv=dataTS$fullvar,
nn=dataTS$fullsize,tt=dataTS$age)
x<-fit3models(PALEO.data)

```

```

#preparing data.frame for PaleoTS() run (DCAaxis1):
fullmean<-bin.meansTS$axis1
fullvar<-bin.sdTS$axis1
dataTS<-data.frame(fullsize,fullmean,fullvar,age)
PALEO.data<-as.paleoTS(mm=dataTS$fullmean,vv=dataTS$fullvar,
nn=dataTS$fullsize,tt=dataTS$age)
x<-fit3models(PALEO.data)

####Evolutionary models (on All excl. lignites and MUDS+SILTS):
bin.dataTS<-data.frame(ages,data226$lithology, Srare,H,axis1) #creates dataframe with ages,
originations and extinctions

SS<-subset(bin.dataTS,data226$lithology=="sandstone")
TT<-subset(bin.dataTS,data226$lithology=="siltstone")
LL<-subset(bin.dataTS,data226$lithology=="lignite")
MM<-subset(bin.dataTS,data226$lithology=="mudstone")

exclig<-rbind(SS,TT,MM) #dataframe all excl. lignites
exclig<-exclig[order(exclig$ages),]
exclig$bin<-cut(exclig$ages,breaks=seq(10.72,18.75,by=0.5),labels=1:16,
include.lowest=T) #adds a 'bin' variable to the dataframe above, bins every 0.5 Ma
exclig[55,"bin"]<-16 #replacing last bin number which was NA for a 16

library(plyr) #to use ddply() in order to calculate means

#calculates means for each variable based on factor bin:
bin.meansTS<-ddply(exclig,.(bin), function(x) data.frame(ages=mean(x$ages),
Srare=mean(x$Srare),axis1=mean(x$axis1),H=mean(x$H)))

#calculates sd for each variable based on factor bin
bin.sdTS<-ddply(exclig,.(bin), function(x) data.frame(ages=sd(x$ages),
Srare=sd(x$Srare),axis1=sd(x$axis1),H=sd(x$H)))

#preparing data.frame for PaleoTS() run (on rar. diversity):
fullsize<-as.numeric(count(exclig$bin)$freq)
fullmean<-bin.meansTS$Srare
fullvar<-bin.sdTS$Srare
age<-bin.meansTS$ages
dataTS<-data.frame(fullsize,fullmean,fullvar,age)
library(paleoTS)
PALEO.data<-as.paleoTS(mm=dataTS$fullmean,vv=dataTS$fullvar,
nn=dataTS$fullsize,tt=dataTS$age)
x<-fit3models(PALEO.data)

```

```

#preparing data.frame for PaleoTS() run (on H' diversity):
fullmean<-bin.meansTS$H
fullvar<-bin.sdTS$H
dataTS<-data.frame(fullsize,fullmean,fullvar,age)
PALEO.data<-as.paleoTS(mm=dataTS$fullmean,vv=dataTS$fullvar,
nn=dataTS$fullsize,tt=dataTS$age)
x<-fit3models(PALEO.data)

#preparing data.frame for PaleoTS() run (DCAaxis1):
fullmean<-bin.meansTS$axis1
fullvar<-bin.sdTS$axis1
dataTS<-data.frame(fullsize,fullmean,fullvar,age)
PALEO.data<-as.paleoTS(mm=dataTS$fullmean,vv=dataTS$fullvar,
nn=dataTS$fullsize,tt=dataTS$age)
x<-fit3models(PALEO.data)

##Time Series analysis on MUDS+SILTS:
MudSilt<-rbind(TT,MM)      #dataframe w MUDS+SILTS
MudSilt<-MudSilt[order(MudSilt$ages),]
MudSilt$bin<-cut(MudSilt$ages,breaks=seq(10.72,18.75,by=0.5),labels=1:16,
include.lowest=T)      #adds a 'bin' variable to the dataframe above, bins every 0.5 Ma

MudSilt[45,"bin"]<-16 #replacing last bin number which was NA for a 16
#Bins with only one sample will be merged with above or below bin (the one with less samples)
MudSilt[5,"bin"]<-3
MudSilt[13,"bin"]<-7

library(plyr) #to use ddply() in order to calculate means

#calculates means for each variable based on factor bin:
bin.meansTS<-ddply(MudSilt,.(bin), function(x) data.frame(ages=mean(x$ages),
Srare=mean(x$Srare),axis1=mean(x$axis1),H=mean(x$H)))

#calculates sd for each variable based on factor bin
bin.sdTS<-ddply(MudSilt,.(bin), function(x) data.frame(ages=sd(x$ages),
Srare=sd(x$Srare),axis1=sd(x$axis1),H=sd(x$H)))

#preparing data.frame for PaleoTS() run (on rar. diversity):
fullsize<-as.numeric(count(MudSilt$bin)$freq)
fullmean<-bin.meansTS$Srare
fullvar<-bin.sdTS$Srare
age<-bin.meansTS$ages
dataTS<-data.frame(fullsize,fullmean,fullvar,age)

```

```
library(paleoTS)
PALEO.data<-as.paleoTS(mm=dataTS$fullmean,vv=dataTS$fullvar,
nn=dataTS$fullsize,tt=dataTS$age)
x<-fit3models(PALEO.data)
```

```
#preparing data.frame for Paleots() run (on H' diversity):
fullmean<-bin.meansTS$H
fullvar<-bin.sdTS$H
dataTS<-data.frame(fullsize,fullmean,fullvar,age)
PALEO.data<-as.paleoTS(mm=dataTS$fullmean,vv=dataTS$fullvar,
nn=dataTS$fullsize,tt=dataTS$age)
x<-fit3models(PALEO.data)
```

```
#preparing data.frame for Paleots() run (DCAaxis1):
fullmean<-bin.meansTS$axis1
fullvar<-bin.sdTS$axis1
dataTS<-data.frame(fullsize,fullmean,fullvar,age)
PALEO.data<-as.paleoTS(mm=dataTS$fullmean,vv=dataTS$fullvar,
nn=dataTS$fullsize,tt=dataTS$age)
x<-fit3models(PALEO.data)
```

### ### Comparison between Miocene and recent diversities (results Chapter 7):

```
Monica1<-read.csv("Data from Behling and Berrio/Monica1.csv", h=T)
Monica1[is.na(Monica1)] <- 0 #replace NAs with zero

Monica2<-read.csv("Data from Behling and Berrio/Monica2.csv", h=T)
Monica2[is.na(Monica2)] <- 0 #replace NAs with zero
Monica3<-read.csv("Data from Behling and Berrio/Monica3.csv", h=T)
Monica3[is.na(Monica3)] <- 0 #replace NAs with zero
Qamor<-read.csv("Data from Behling and Berrio/Quebrada del Amor.csv", h=T)
Qamor[is.na(Qamor)] <- 0 #replace NAs with zero
```

```
library(vegan)
```

### #within-sample rarefied diversity Holocene (before running, run read.csv again)

```
Monica1R<-rarefy(Monica1[-1],226,se=TRUE)
Monica2<-Monica2[rowSums(Monica2[-1])>225,] #Monica 2 has samples below cutoff
Monica2R<-rarefy(Monica2[-1],226,se=TRUE)
Monica3R<-rarefy(Monica3[-1],226,se=TRUE)
Qamor<-Qamor[rowSums(Qamor[-1])>225,]#Qamor has samples below cutoff
QamorR<-rarefy(Qamor[-1],226,se=TRUE)

quat226<-c(Monica1R[1,],Monica2R[1,],Monica3R[1,],QamorR[1,])##TOTAL HOLOCENE
```

```

quat226<-as.numeric(quat226)
mean(quat226) #39.6 mean divers
wilcox.test(Srare[1:37],quat226)
wilcox.test(Srare[38:67],quat226)

#Within-sample H' diversity Holocene:
Monica1H<-diversity(Monica1[-1])
Monica2<-Monica2[rowSums(Monica2[-1])>225,] #Monica 2 has samples below cutoff
Monica2H<-diversity(Monica2[-1])
Monica3H<-diversity(Monica3[-1])
Qamor<-Qamor[rowSums(Qamor[-1])>225,]#Qamor has samples below cutoff
QamorH<-diversity(Qamor[-1])

quat226<-c(Monica1H,Monica2H,Monica3H,QamorH)##TOTAL HOLOCENE
quat226<-as.numeric(quat226)
mean(quat226) #2.7 mean divers
wilcox.test(H[1:37],quat226)
wilcox.test(H[38:67],quat226)

##checking evenness of Quater. sites:
S1<-specnumber(Monica1)
S2<-specnumber(Monica2)
S3<-specnumber(Monica3)
S4<-specnumber(Qamor)

J1<-Monica1H/log(S1)
J2<-Monica2H/log(S2)
J3<-Monica3H/log(S3)
J4<-QamorH/log(S4)
J<-c(J1,J2,J3,J4)
mean(J)
min(J)

#'violin' plot: (construct data matrix of spp+ DCA1 taxa scores and plots Fig. 7.7)
new_data<-read.csv("data_violin_RangeT.csv",h=T)
new_data[is.na(new_data)] <- 0
S_pos<-new_data[1:67,2:2]
S_pre<-new_data[1:67,3:3]
S_thr<-new_data[1:67,4:4]
df<-data.frame(S_pos, S_pre, S_thr)
library(rioja)

y.tks<-seq(10.7,18.8,0.5)

```



```

par(tcl=-.25)
x<-strat.plot (df,yvar=ages,scale.percent=T,
  graph.widths=1, minmax=NULL,
  scale.minmax = F, xLeft = 0.1, xRight = .5,
  yBottom = 0.07, yTop = 0.8, title = "", cex.title=1.2,
  y.axis=TRUE, min.width = 5, ylim = NULL, y.rev = T,
  y.tks=y.tks, ylabel = "Ages(Ma)", cex.ylabel=1, cex.yaxis=.8,
  xspace = 0.01, wa.order = "none",plot.line=F,
  col.line = "black", lwd.line=1,plot.bar=F,
  lwd.bar = 1, col.bar = "grey", sep.bar = FALSE,
  plot.poly =T,col.poly="grey",col.poly.line="grey30",
  lwd.poly = 1, x.names=NULL, cex.xlabel = .88, srt.xlabel=45,
  cex.axis=.8, clust.width=0.1,
  orig.fig=NULL)

addZone(x,13.72,col="grey50",lty=3) #MM top
addZone(x,14.15,col="grey50",lty=3) #MM bottom
addZone(x,17.8,col="grey50",lty=3)#EM top
addZone(x,18.43,col="grey50",lty=3)#EM bottom

##Zachos curve for this plot:
data_z<-read.csv("zachos2008.csv",head=T)
plot(data_z$d180.5pt,data_z$Age,ylim=c(18.7,10.7), xlim=c(3,1.3),type="l",
col="grey30",lwd=1.5,xlab="d180",ylab="")

```

Results of the Post-hoc TukeyHSD multiple comparisons of means (95% family-wise confidence level) for ANOVA testing lithology vs. diversity metrics. Boldface means significant differences.

a) Rarefied diversity:

```

Fit: aov(formula = sqrt(Srare) ~ lithology * strata, data = litho.data)

$lithology
      diff      lwr      upr      p adj
mudstone-lignite  0.6144801 -0.05424940 1.2832096 0.0825708
siltstone-lignite  1.1278650  0.38385875 1.8718712 0.0009789
sandstone-lignite  1.3039071  0.46970963 2.1381046 0.0006496
siltstone-mudstone  0.5133849 -0.09334506 1.1201148 0.1252095
sandstone-mudstone  0.6894270 -0.02503879 1.4038929 0.0623881
sandstone-siltstone 0.1760422 -0.60932881 0.9614131 0.9339280

$strata
      diff      lwr      upr      p adj
younger-older 0.5978294 0.2371717 0.9584871 0.001562

$`lithology:strata`
      diff      lwr      upr      p adj
lignite:older-lignite:younger  0.37389534 -2.044624015 2.792415 0.9996865
mudstone:older-lignite:younger  0.48382691 -1.919139105 2.886793 0.9982498

```

siltstone:older-lignite:younger	0.85383807	-1.647248254	3.354924	0.9600036
mudstone:younger-lignite:younger	1.34184730	-1.044973182	3.728668	0.6444602
sandstone:older-lignite:younger	1.40582427	-1.430141051	4.241790	0.7728189
sandstone:younger-lignite:younger	1.70684957	-0.749168436	4.162868	0.3762490
siltstone:younger-lignite:younger	1.84066092	-0.587914685	4.269237	0.2694982
mudstone:older-lignite:older	0.10993157	-0.838689766	1.058553	0.9999547
siltstone:older-lignite:older	0.47994273	-0.695246434	1.655132	0.9014362
<b>mudstone:younger-lignite:older</b>	<b>0.96795196</b>	<b>0.061007205</b>	<b>1.874897</b>	<b>0.0284750</b>
sandstone:older-lignite:older	1.03192893	-0.748053113	2.811911	0.6082942
<b>sandstone:younger-lignite:older</b>	<b>1.33295424</b>	<b>0.257007558</b>	<b>2.408901</b>	<b>0.0058555</b>
<b>siltstone:younger-lignite:older</b>	<b>1.46676559</b>	<b>0.455026355</b>	<b>2.478505</b>	<b>0.0006698</b>
siltstone:older-mudstone:older	0.37001116	-0.772827135	1.512849	0.9699598
mudstone:younger-mudstone:older	0.85802039	-0.006594314	1.722635	0.0531731
sandstone:older-mudstone:older	0.92199736	-0.836793665	2.680788	0.7200251
<b>sandstone:younger-mudstone:older</b>	<b>1.22302267</b>	<b>0.182507865</b>	<b>2.263537</b>	<b>0.0107452</b>
<b>siltstone:younger-mudstone:older</b>	<b>1.35683402</b>	<b>0.382859649</b>	<b>2.330808</b>	<b>0.0012236</b>
mudstone:younger-siltstone:older	0.48800923	-0.620478806	1.596497	0.8611304
sandstone:older-siltstone:older	0.55198620	-1.338657344	2.442630	0.9831831
sandstone:younger-siltstone:older	0.85301151	-0.397531653	2.103555	0.4003633
siltstone:younger-siltstone:older	0.98682286	-0.208925115	2.182571	0.1791372
sandstone:older-mudstone:younger	0.06397697	-1.672690018	1.800644	1.0000000
sandstone:younger-mudstone:younger	0.36500228	-0.637662876	1.367667	0.9440526
siltstone:younger-mudstone:younger	0.49881363	-0.434616834	1.432244	0.7002793
sandstone:younger-sandstone:older	0.30102531	-1.529582436	2.131633	0.9995288
siltstone:younger-sandstone:older	0.43483665	-1.358785301	2.228459	0.9944162
siltstone:younger-sandstone:younger	0.13381135	-0.964553298	1.232176	0.9999364

## B) H' diversity:

Fit: aov(formula = H ~ lithology \* strata, data = litho.data)

\$lithology

	diff	lwr	upr	p adj
mudstone-lignite	0.23594426	-0.10507244	0.5769610	0.2701357
<b>siltstone-lignite</b>	<b>0.43909364</b>	<b>0.05968978</b>	<b>0.8184975</b>	<b>0.0170751</b>
<b>sandstone-lignite</b>	<b>0.46853541</b>	<b>0.04313877</b>	<b>0.8939321</b>	<b>0.0253795</b>
siltstone-mudstone	0.20314938	-0.10625083	0.5125496	0.3146567
sandstone-mudstone	0.23259115	-0.13174867	0.5969310	0.3391978
sandstone-siltstone	0.02944177	-0.37105592	0.4299395	0.9973692

\$strata

	diff	lwr	upr	p adj
<b>younger-older</b>	<b>0.2115019</b>	<b>0.02758555</b>	<b>0.3954183</b>	<b>0.024935</b>

\$`lithology:strata`

	diff	lwr	upr	p adj
lignite:older-lignite:younger	0.24921766	-0.984099422	1.4825347	0.9982092
mudstone:older-lignite:younger	0.28686655	-0.938519148	1.5122522	0.9954945
siltstone:older-lignite:younger	0.48485960	-0.790562274	1.7602815	0.9303606
sandstone:older-lignite:younger	0.51696066	-0.929231802	1.9631531	0.9490638
mudstone:younger-lignite:younger	0.60863465	-0.608517680	1.8257870	0.7650683
sandstone:younger-lignite:younger	0.74199100	-0.510448416	1.9944304	0.5819083
siltstone:younger-lignite:younger	0.77715330	-0.461291943	2.0155985	0.5090664
mudstone:older-lignite:older	0.03764889	-0.446097866	0.5213957	0.9999970
siltstone:older-lignite:older	0.23564194	-0.363642440	0.8349263	0.9177890
sandstone:older-lignite:older	0.26774301	-0.639953786	1.1754398	0.9821651
mudstone:younger-lignite:older	0.35941699	-0.103076913	0.8219109	0.2411265
sandstone:younger-lignite:older	0.49277334	-0.055902616	1.0414493	0.1090397
<b>siltstone:younger-lignite:older</b>	<b>0.52793564</b>	<b>0.012002088</b>	<b>1.0438692</b>	<b>0.0413216</b>
siltstone:older-mudstone:older	0.19799305	-0.384794098	0.7807802	0.9610248
sandstone:older-mudstone:older	0.23009411	-0.666796379	1.1269846	0.9921339
mudstone:younger-mudstone:older	0.32176810	-0.119139716	0.7626759	0.3147029
sandstone:younger-mudstone:older	0.45512445	-0.075483123	0.9857320	0.1445454
siltstone:younger-mudstone:older	0.49028675	-0.006388719	0.9869622	0.0554517
sandstone:older-siltstone:older	0.03210107	-0.932027244	0.9962294	1.0000000
mudstone:younger-siltstone:older	0.12377505	-0.441495276	0.6890454	0.9970260
sandstone:younger-siltstone:older	0.25713140	-0.380579534	0.8948423	0.9072283
siltstone:younger-siltstone:older	0.29229370	-0.317474585	0.9020620	0.8010490
mudstone:younger-sandstone:older	0.09167398	-0.793934418	0.9772824	0.9999790
sandstone:younger-sandstone:older	0.22503033	-0.708482888	1.1585436	0.9946073
siltstone:younger-sandstone:older	0.26019263	-0.654459794	1.1748451	0.9855223
sandstone:younger-mudstone:younger	0.13335635	-0.377949900	0.6446626	0.9913165
siltstone:younger-mudstone:younger	0.16851865	-0.307481567	0.6445189	0.9515555
siltstone:younger-sandstone:younger	0.03516230	-0.524945637	0.5952702	0.9999993

c) DCA axia 1:

Fit: aov(formula = sqrt(axis1) ~ lithology \* strata, data = litho.data)

\$lithology

	diff	lwr	upr	p adj
siltstone-sandstone	0.1313210	-0.10407913	0.3667211	0.4589390
<b>mudstone-sandstone</b>	<b>0.2414952</b>	<b>0.02734759</b>	<b>0.4556429</b>	<b>0.0211041</b>
<b>lignite-sandstone</b>	<b>0.5483123</b>	<b>0.29827735</b>	<b>0.7983473</b>	<b>0.0000017</b>
mudstone-siltstone	0.1101742	-0.07168161	0.2920301	0.3855842
<b>lignite-siltstone</b>	<b>0.4169913</b>	<b>0.19398948</b>	<b>0.6399931</b>	<b>0.0000389</b>
<b>lignite-mudstone</b>	<b>0.3068171</b>	<b>0.10637802</b>	<b>0.5072561</b>	<b>0.0008613</b>

\$strata

	diff	lwr	upr	p adj
<b>older-younger</b>	<b>0.381128</b>	<b>0.2730277</b>	<b>0.4892283</b>	<b>0</b>

\$`lithology:strata`

	diff	lwr	upr	p adj
siltstone:younger-sandstone:younger	0.001115733	-0.3280984	0.3303298	1.0000000
mudstone:younger-sandstone:younger	0.077810468	-0.2227195	0.3783404	0.9916889
sandstone:older-sandstone:younger	0.324344018	-0.2243461	0.8730342	0.5846405
lignite:younger-sandstone:younger	0.368634654	-0.3675104	1.1047797	0.7637788
<b>siltstone:older-sandstone:younger</b>	<b>0.521313265</b>	<b>0.1464865</b>	<b>0.8961400</b>	<b>0.0012533</b>
<b>mudstone:older-sandstone:younger</b>	<b>0.587660773</b>	<b>0.2757861</b>	<b>0.8995355</b>	<b>0.0000047</b>
<b>lignite:older-sandstone:younger</b>	<b>0.635412619</b>	<b>0.3129179</b>	<b>0.9579073</b>	<b>0.0000017</b>
mudstone:younger-siltstone:younger	0.076694735	-0.2030834	0.3564729	0.9883370
sandstone:older-siltstone:younger	0.323228286	-0.2143761	0.8608326	0.5635771
lignite:younger-siltstone:younger	0.367518922	-0.3604008	1.0954387	0.7562881
siltstone:older-siltstone:younger	0.520197532	0.1617946	0.8786004	0.0006577
<b>mudstone:older-siltstone:younger</b>	<b>0.586545040</b>	<b>0.2946146</b>	<b>0.8784755</b>	<b>0.0000011</b>
<b>lignite:older-siltstone:younger</b>	<b>0.634296887</b>	<b>0.3310471</b>	<b>0.9375466</b>	<b>0.0000004</b>
sandstone:older-mudstone:younger	0.246533550	-0.2739996	0.7670667	0.8105383
lignite:younger-mudstone:younger	0.290824186	-0.4245802	1.0062286	0.9035598
<b>siltstone:older-mudstone:younger</b>	<b>0.443502797</b>	<b>0.1112544</b>	<b>0.7757512</b>	<b>0.0022405</b>
mudstone:older-mudstone:younger	0.509850304	0.2506984	0.7690023	0.0000017
<b>lignite:older-mudstone:younger</b>	<b>0.557602151</b>	<b>0.2857626</b>	<b>0.8294417</b>	<b>0.0000006</b>
lignite:younger-sandstone:older	0.044290636	-0.8057365	0.8943178	0.9999998
siltstone:older-sandstone:older	0.196969247	-0.3697155	0.7636540	0.9560059
mudstone:older-sandstone:older	0.263316754	-0.2638477	0.7904812	0.7660604
lignite:older-sandstone:older	0.311068601	-0.2224474	0.8445846	0.6014210
siltstone:older-lignite:younger	0.152678611	-0.5969748	0.9023321	0.9981174
mudstone:older-lignite:younger	0.219026118	-0.5012176	0.9392699	0.9787957
lignite:older-lignite:younger	0.266777965	-0.4581276	0.9916835	0.9408542
mudstone:older-siltstone:older	0.066347507	-0.2761967	0.4088917	0.9986341
lignite:older-siltstone:older	0.114099354	-0.2381414	0.4663401	0.9698788
lignite:older-mudstone:older	0.047751847	-0.2365795	0.3320832	0.9994588

#### **9.4 Sedimentology and Sequence Stratigraphy analysis of core 1-AS-105-AM (the text and analysis below are from Jaramillo *et al. in prep*)**

Methods:

Saltarin (Jaramillo *et al. in prep*) and 105-AM cores were described at a scale of 1:50 for identification of grain-size trends, sedimentary structures, clast composition, thickness of lamination, bioturbation patterns, and macrofossil identification, which are the support of identification of individual lithofacies. The association of lithofacies within a vertical and conformable succession is the support for depositional environment interpretation, following the criteria James and Dalrymple (2010) and Miall (1996). Sequence stratigraphy analysis follows the criteria described in Catuneanu *et al.* (2009) for definition of flooding surfaces, maximum flooding surfaces and sequence boundaries, as well as the identification of aggradational, progradational and retrogradational stacking patterns of deposition for marginal deposits. For fluvial strata, we used the terms “low accommodation” and “high accommodation” system tracts, as discussed in Catuneanu *et al.* (2009). For homogeneous fine-grained strata accumulated in shallow waters, we used a combination of lithofacies and biostratigraphy data to identify the stratigraphic surfaces of correlation. The detailed sedimentological, biostratigraphic and sequence stratigraphic analyses allowed the identification of stratigraphic sequences of less than 1 Ma of duration. All sedimentological, biostratigraphic and stratigraphic data are storage and displayed using SDAR software (Ortiz *et al.*, 2015).

Well 1-AS-105-AM drilled the Solimões (26.2 to 332.7 m) and Ramón formations (332.7-405 m). Three informal members were identified within the Solimões Formation (Sedimentary log is attached below):

- The lower member (332.7 – 267.5 m) includes three sequences that consists of very thick beds of massive to laminated claystones, siltstones and carbonaceous siltstones passing upsection to medium to thick bedded sublitharenites, locally with cross beds, and thin to medium beds of lignite. A similar succession is documented for the uppermost sequence for the Ramón Formation (358.8-332.7), but the arenites are quartzose in composition.

- The middle member (168.2-267.5 m) includes two very thick sequences that are characterized by laminated and carbonaceous siltstones in the retrogradational segment, with an important increment of decimeter- to meter-scale lignite beds interbedded with siltstones in the aggradational to progradational segment, and lithic-bearing, upward fining and coarsening sandstones and paleosols are part of the progradational interval.

- The upper member (26.2-168.2 m) includes five sequences whose lower retrogradational segment includes gastropods, bivalves and other shell fragments in fine-grained laminated, bioturbated to massive siliciclastic strata and biomicrites that passes upsection to upward-fining sublitharenites with thin to medium beds of lignite; the abundance of fossil content decreases upsection, whereas thickness of sandstone interbeds increases upsection.

The two marine incursions are recorded in claystones with organic matter of the lower member (284-293 m) and in mollusk-rich carbonaceous siltstones of the upper member (96-98 m). These marine incursions correspond to the retrogradational segment and maximum flooding surfaces of two major sequences. The lower sequence involves the lower and middle member of the Solimoes Formation that accumulated mainly in marginal plains with anoxic conditions that allowed the preservation of organic material and development of lignite. The upper sequence accumulated in oxygen-rich marginal settings with broad development of lacustrine systems that allowed the record of gastropods and bivalves. Both sequences have the record of thin fluvial conditions to the top.

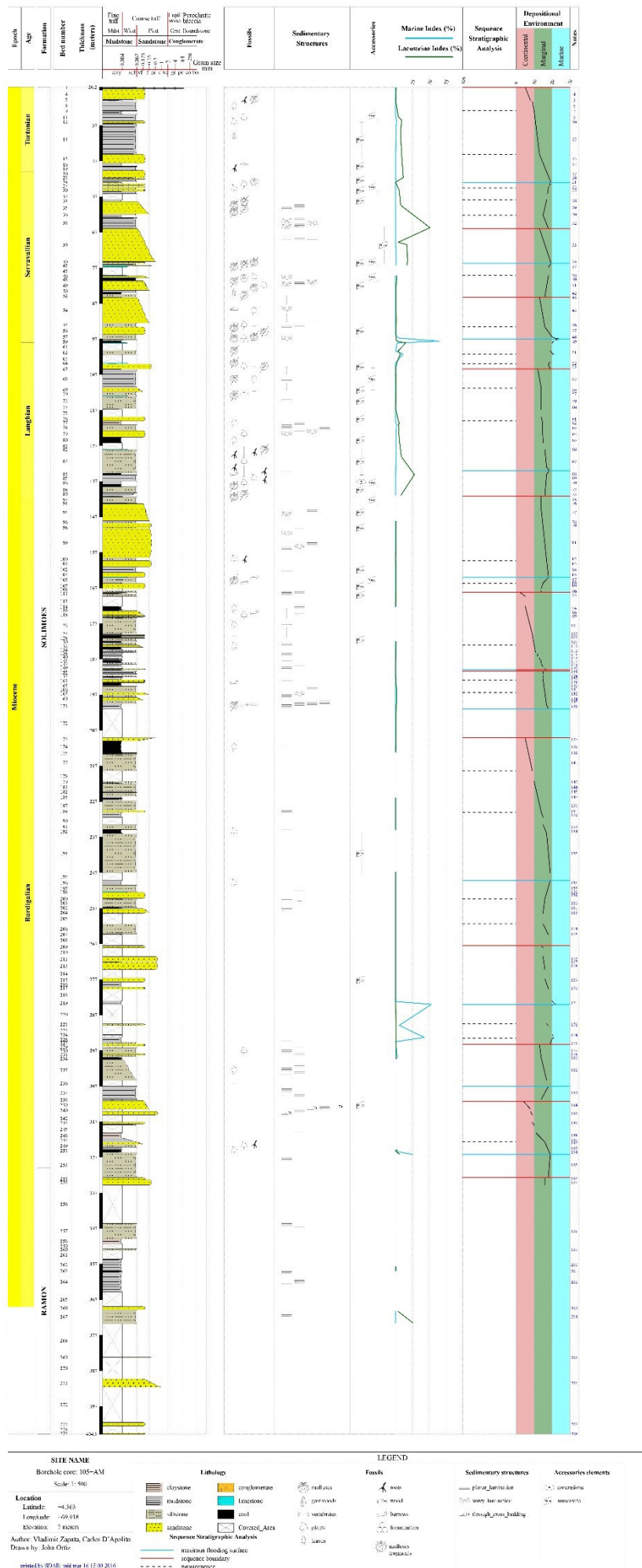
A summary of lithology associations, depositional environment interpretation and stacking patterns of stratigraphic sequences identified in the Ramón and Solimoes units from meters 26.2 to 358.8, with emphasis in the two marine intervals documented in this study, is given below:

Unit (depth interval in meters)	Lithofacies association	Marine, lacustrine and pollen indicators	Depositional environment interpretation	Sequence stratigraphy analysis
<b>Solimões Formation (26.2-53.1 m)</b>	From base to top: 45-53.1 m: upward-coarsening siltstones to fine-grained litharenites and one medium-bed lignite; 32.8-45 m: silty mudstone; 26.2-32.8m: calcareous siltstone grading upsection to <b>upward-fining conglomeratic sublitharenite</b>	Lacustrine 0 - 11.5%; Marine 0 - 1.3%; Gastropods and bivalves at the base of the interval. Macroscopic organic matter and plant remains. Excellent palynomorph recovery.	Marginal: extensive development of plains surrounding lacustrine systems. <b>Advance of fluvial channels to the top</b>	Base is a maximum flooding surface. Stacking pattern of three parasequences indicate aggradation at the base to <b>progradation toward the top</b> .
<b>Solimões Formation (53.1-66 m)</b>	Upward-coarsening laminated siltstones grading to fine-grained sublitharenites	Lacustrine 0 - 51.2%; Gastropods, bivalves and shell fragments. Macroscopic organic matter and plant remains. Moderate to excellent palynomorph recovery.	Marginal: deltaic plains with shallow channels ending in shallow lacustrine systems	Base is a sequence boundary. Parasequences defined in this interval show a retrogradational pattern of deposition, and allow the identification of a maximum flooding surface at the top
<b>Solimões Formation (66-85.2 m)</b>	From base to top: 75.7-85.2 m: Calcareous siltstones and fine-grained sandstones, biomicrite and two thick-bedded lignite; 66-75.7 m: upward-fining medium-grained sublitharenite to laminated siltstone	Lacustrine indicators ranges from 1.3 to 17.1 %. Gastropods, bivalves and shell fragments. Macroscopic organic matter and plant remains. Moderate to excellent palynomorph recovery.	Marginal: Subaqueous marginal system (75.7-85.2) with advance of deltaic plains with shallow channels (66-75.7)	A complete sequence is defined for this interval; fossil-rich interval records the retrogradation and the Maximum flooding surface, whereas the sandstone interval records the progradation of the system
<b>Solimões Formation (85.2-105.4 m)</b>	From base to top: 95.7-105.4 m: fossil-rich interval with fine-grained sandstones, siltstones, biomicrite and a medium bedded peat interval; 85.2-95.7 m is a upward-fining, fine-grained sandstones to planar- to wavy-laminated siltstone, and a thin bed of lignite at the top	Marine incursion with 64.8% at 97.6 m and ranging from 3.5-11% from 96.7 to 101.2 m. Lacustrine indicators ranging from 0.3 - 14.9%. Gastropods and bivalves fragments; Macroscopic organic matter at different levels. Excellent palynomorph recovery.	Marginal to marine: Subaqueous marginal system (95.7-105.4 m) with a short period of marine incursion. Upper segment records the advance of deltaic plains with shallow channels (85.2 - 95.7)	A complete sequence is defined for this interval; fossil-rich interval records the retrogradational stacking pattern. The maximum flooding surface is recorded by the marine incursion, whereas the upper sandstone segment records the progradational stacking pattern.
<b>Solimões Formation (105.4-141.1 m)</b>	From base to top: 141.1-137 m: Laminated claystones and siltstones with shell fragments. 120-137 m: planar to wavy laminated fine-grained sublitharenite, siltstone and planar laminated mudstone; 105.4-120 m: upward-fining successions of fine-grained sublitharenite and siltstones with thin lignite beds at the top, and localized shell fragments	Lacustrine indicators from 120.3 to 125.3 m ranges from 4.1 - 5.7%; from 130.1 to 135.1 m ranges from 8-28%: with 1.3% of marine indicators at 120.9 m; localized shell fragments. Macroscopic organic matter in the 120-127 m interval. Excellent palynomorph recovery.	Marginal: dominantly subaqueous lacustrine and marginal plains with migration of shallow channels and adjacent plains with lignite accumulation	A complete sequence is defined for this interval; lower fossiliferous interval records the retrogradation with the maximum flooding surface at 134 m (in the interval of high lacustrine indicators). The upper segment records progradation of marginal plains over lacustrine system

<b>Solimões Formation (141.1-168.2 m)</b>	From base to top: 164-168.2 m: a coarsening-upward siltstone to litharenite and a meter scale siltstone with shell fragments. 141.1-164 m: interbedding of fine- to medium grained litharenites to sublitharenites, thickening upsection and localized planar to wavy lamination to the top; laminated to bioturbated mudstones, localized paleosol development.	Moderate to excellent palynomorph recovery. 164 to 165.7 m: gastropods, bivalves, and bioturbation; abundant organic matter in 161 to 162.6 m.	Marginal plains with record of migrating channels on floodplains with short periods of subaerial exposure	A complete sequence is defined by a retrogradational stacking pattern at the base with the maximum flooding surface at the interval with shell fragments (the thinnest in comparison with the overlying two sequences). The upper segment records the progradation of migrating channels on marginal plains.
<b>Solimões Formation (168.2-209.1 m)</b>	From base to top: 199.5 to 200.9 m: laminated siltstones, bioturbated with shell fragments; 168.2-199.5 m: dominates laminated and carbonaceous siltstone, locally bioturbated followed by <b>decimeter to meter-thick lignites interbedded with meter-scale upward-fining fine-grained sublitharenites. Two thin layers of paleosol toward the top.</b>	Moderate to excellent palynomorph recovery. 199.5 to 200.9 m: bivalves, gastropods, shell fragments.	Migration of: (1) subaqueous marginal lacustrine at the base, to (2) a marginal plains with abundant ponds and oxbows, and (3) <b>to a continental fluvial system with channels and subaerial exposure of the adjacent floodplains</b>	A complete sequence is defined by the retrogradation of Siltstones with shell fragments recording the maximum flooding surface; lignite-rich interval records the aggradation, <b>whereas arenites and paleosols record the progradation of the continental system.</b>
<b>Solimões Formation (209.1-249.2 m)</b>	Fine-grained succession with massive to locally laminated and bioturbated siltstones; carbonaceous siltstone to the top; <b>decimeter to meter-thick lignites</b> interbedded with meter-scale upward-coarsening sublitharenites, locally laminated.	Moderate to excellent palynomorph recovery.	Marginal coastal plains with presence of ponds, oxbows and channel migration toward the top	Thick fine-grained succession at the base records the maximum flooding surface and onset of aggradation. Lignite and channel interbeds record the progradation of the system. Top is a sequence boundary,
<b>Solimões Formation (249.2-267.5 m)</b>	Siltstones changing from massive at the base to laminated and organic rich to the top. An upward-fining litharenite and a thin-bedded paleosol layer to the top	Excellent palynomorph recovery.	Marginal plains with channel at the base a more subaqueous conditions to the top	Base is a sequence boundary. This succession records an increase of base level (high accommodation stacking pattern) and retrogradational pattern, allowing the thick record of fine-grained successions.
<b>Solimões Formation (267.5-295.2 m)</b>	From base to top: 277.7-295.2: Poor preserved segment of claystones with organic matter grading to sublitharenite with paleosol development and locally bioturbated. 267.5-277.7: Mainly sublitharenites with a upward-coarsening trend and localized organic matter	Marine indicators at 284 (53.4%), 289.9 (5.4%), 293.3 (42.8%). All the succession has an excellent palynomorph recovery.	Lower interval represents a marine flooded marginal plain, whereas the sandy interval at the top records the migration of a sandy deltaic plain	Marine incursions in the lower interval records the retrogradational stacking pattern and maximum flooding system at 284 m, whereas the sandy interval records the progradation of marginal conditions

<b>Solimões Formation (295.2-311 m)</b>	Four-meter thick claystone at the base passing upsection to laminated carbonaceous siltstones with a medium bed of lignite, and a medium-bedded sublitharenite at the top.	Marine and lacustrine indicators in 298.9-299.3 m are less than 2.5%. Palynomorph recovery increases upsection	Marginal subaqueous system	Lower interval of claystones records the retrogradational (high accommodation) stacking pattern and maximum flooding surface, whereas the upper interval shows the progradation of a higher energy subaqueous marginal system
<b>Solimões Formation (311-332.7 m)</b>	From base to top: 323.3-332.7 m: seven-meter thick laminated siltstones at the base passing to a medium bed of lignite to the top interbedded with the siltstones. 311-323.3 m: <b>upward-fining medium-grained sublitharenites with cross beds and planar lamination.</b>	Marine indicators (25.6%) and lacustrine indicators (6.2%) in 326.2 m; minor influence in 324.9 (1 and 2.3%). Poor to moderate palynomorph recovery.	Marginal conditions with a short period of marine incursions at the base changing <b>to a fluvial-deltaic system to the top</b>	This succession is a complete sequence with retrogradational (high accommodation) stacking pattern and maximum flooding surface in the lower interval passing to a <b>progradational fluvial deltaic system to the top</b>
<b>Ramón Formation (332.7-358.8 m)</b>	Three meter-thick claystone at the base passing to siltstones in the middle and <b>medium- to fine- to medium grained quartzarenites to the top</b>	Lacustrine indicators of 0.3% at 357.7m. Poor to moderate palynomorph recovery.	Marginal at the base passing <b>to fluvial channel systems to the top</b>	This succession is a complete sequence with retrogradational (high accommodation) stacking pattern and maximum flooding surface in the lower marginal interval passing to a <b>progradational fluvial system to the top</b>





Footnote	base_depth	top_depth	Comments / Notes
1	26.45	26.2	Sparse oxidized organic matter.
2	26.6	26.45	Polymict conglomerate and sublitharenite. Clasts up to 1.5 cm wide
3	26.7	26.6	Sparse oxidized organic matter.
4	29.6	26.7	Sublitharenite. Sparse fragments of organic matter– quartz grains and lithics.
5	30	29.8	Organic rich.
6	32.8	30.2	Organic rich– carbonized plant remains. Light in weight– possible bioturbation– slight content of carbonate towards the base.
7	32.95	32.8	Abundant muscovite.
8	33.8	32.95	Sparse organic matter.
9	35.7	33.8	Organic matter and abundant fragments of leaves and carbonized plant remains. Sparse lithics.
10	36.3	35.7	Sublitharenite. Organic matter and carbonized plant remains.
11	36.6	36.3	Abundant organic matter.
12	45.1	36.6	Organic matter.
13	47.6	45.1	Sublitharenite. Abundant organic matter and oxidized nodules. Low content of carbonate.
14	48.3	47.6	Organic rich and sparse fragments of carbonized wood.
15	48.4	48.3	Abundant organic matter.
16	48.6	48.4	Lignite.
17	51.6	49.6	Sublitharenite. First 20 cm are slightly carbonated. Abundant organic matter– lithics and micas. Frequent oxidation.
18	51.8	51.6	Organic matter.
19	52.1	51.8	Sublitharenite. Organic matter.
20	52.7	52.1	Organic matter.
21	53.1	52.7	Milimetric fragments of bivalves and gastropods (matrix is non calcareous).
22	53.8	53.3	Sublitharenite. Abundant organic matter– plant bioturbation– sulfur. Contains carbonized plant remains.
23	54.5	54.1	Sublitharenite. Organic matter.
24	54.9	54.5	Abundant organic matter and carbonized plant remains.
25	55.4	54.9	Sublitharenite. Abundant organic matter.
26	55.6	55.4	Lignite (oxidized).
27	56.1	55.6	Abundant organic matter. Possible hard ground.
28	58.4	57.9	Organic matter and shell fragments.
29	61.8	58.4	Sublitharenite. Slightly calcareous– sporadic shell fragments. Sporadic organic matter and sulfur. Planar laminations 1 to 3 mm.
30	62.2	61.8	Organic matter and sulfur.
31	62.9	62.2	Thin planar and slightly wavy lamination– 1 to 3 mm. Organic matter and sulfur.
32	66	62.9	Slight oxidation. Sporadic organic matter and millimetric shell fragments. Thin planar stratification– clay laminae of up to 2 mm.
33	75.2	66	Sublitharenite. Contains lithics– quartz and organic matter. Thin planar and slightly wavy stratification.
34	75.4	75.2	Shell fragments– opaques.
35	75.7	75.4	Sublitharenite. Organic matter.
36	76.3	75.7	Slightly calcareous– shell fragments.
37	76.8	76.4	Biomicrite. Bivalves and millimetric calcite veins.
38	79.3	79.1	Biomicrite– impure– contains terrigenous mud and abundant shell fragments.
39	79.8	79.3	Sublitharenite. Abundant fragments of shells and carbonized plant remains. Thin slightly wavy lamination.
40	80.6	79.8	Peat. Multiple shell fragments.
41	83.3	80.6	Sublitharenite. Abundant fragments of shells and carbonized plant remains. Thin slightly wavy lamination.
42	84.4	83.85	Peat. Abundant bivalves in life position– some fragments– and gastropods.

43	85.2	84.4	Shell fragments.
44	85.4	85.2	Lignite. Contains sulfur.
45	92.5	85.4	Sublitharenite to silt– very thin wavy to irregular lamination– abundant carbonized plant remains. Contains sulfur and organic matter.
46	93.6	92.5	Abundant carbonized plant remains and sulfur.
47	95.7	93.6	Sublitharenite. Quartz– lithics– opaques. Sporadic shell fragments and molluscs.
48	97.2	95.7	Bivalve fragments and little organic matter.
49	98	97.5	Peat. Calcareous– shell fragments– thin way stratification– sulfur– opaques.
50	98.2	98	Biomicrite. Shell fragments and foraminifera.
51	101.4	100.2	Multiple shell fragments (bivalve and gastropod)– opaques. Color has reddish stains.
52	103.9	103.65	Biomicrite– shell fragments– millimetric calcite veins.
53	105.4	104	Sublitharenite. Abundant shell fragments– opaques– carbonized plant remains.
54	105.6	105.4	Lignite. Contains sulfur.
55	110.8	105.6	Abundant shell fragments and carbonized plant remains– sulfur. Very thin planar lamination.
56	111.8	110.8	Sublitharenite.
57	112.9	111.8	Micas– opaques– organic matter– carbonized wood.
58	113.05	112.9	Impure micrite– with shell fragments.
59	115.8	113.05	Thin planar lamination.
60	116.6	115.8	Sulfur.
61	120	118.9	Sublitharenite. Opaques– sporadic organic matter.
62	121.1	120	Peat. Carbonized plant remains.
63	122.8	121.1	Sporadic organic matter– micas.
64	124.6	122.8	Sublitharenite. Thin planar to slightly wavy lamination– non–continuous. Sporadic organic matter– carbonized plant remains– little sulfur.
65	126.2	124.6	Fisile– organic matter– carbonized plant remains.
66	128.1	128	Biomicrite. Shell fragments and calcite veins. Contains terrigenous silt.
67	134.7	128.1	Bioturbation by roots (centimetric)– carbonized plant remains– opaques (very fine sand).
68	135.2	134.7	Peat. Thin planar lamination.
69	137	135.2	Peat. Organic matter– bioturbation by roots– carbonized plant remains.
70	137.8	137	Peat. Organic matter– bioturbation– carbonized plant remains and sporadic intraclasts.
71	138.5	137.8	Peat. Thin planar lamination– fragmented and few entire bivalves and gastropods.
72	140.2	138.5	Organic matter.
73	141.1	140.2	Millimetric bivalves and gastropods– organic matter.
74	141.3	141.2	Shell fragments.
75	143.1	141.4	Little organic matter– muscovite and some opaques.
76	143.3	143.1	Micrite.
77	148.1	143.3	Sublitharenite. Opaques– quartz– lithics– little organic matter.
78	148.8	148.1	Oxidized organic matter. Sporadic fragments of mica.
79	149.9	148.8	Sublitharenite. Quartz– opaques– lithics and organic matter.
80	150.1	149.9	Carbonized organic matter. (possible paleosoil).
81	158.4	150.1	Sublitharenite. Quartz– opaques– lithics and organic matter.
82	159.3	158.4	Carbonized plant remains– organic matter– lithics– plant bioturbation by roots.
83	161	159.3	Sublitharenite– 80% quartz grains– lithics– micas– sporadic organic matter.
84	162.6	161	Planar stratification– slightly wavy– laminae 3 mm to 1 cm. Abundant organic matter– some lithics.

85	163.9	162.6	Sublitharenite. Quartz– opaques– lithics– poor organic matter– and micas.
86	164	163.9	Siderite.
87	165.4	164	Shell fragments and entire millimetric shells. organic matter.
88	165.7	165.4	Shell fragments. Centimetric burrow filled with top lithology.
89	167.1	165.7	Sublitharenite. Organic matter.
90	168.2	167.7	Thin planar lamination. Organic matter– opaques.
91	168.35	168.2	Siderite.
92	168.7	168.35	Slightly calcareous– very thin lamination.
93	169.3	168.7	Organic matter– lithics– thin lamination 1 to 3 mm.
94	173	172.3	Lignite with silt laminae (up to 1 cm). Carbonized plant remains.
95	173.4	173	Peat.
96	174.4	173.4	Sublitharenite. Burrows filled with top lithology.
97	174.5	174.4	Siderite.
98	174.7	174.5	Carbonized plant remains– organic matter. Thin lamination.
99	175.1	174.7	Sublitharenite. Quartz and opaques.
100	175.3	175.1	Lignite (pure). Carbonized plant remains and sulfur.
101	179.7	175.3	Organic matter and carbonized plant remains.
102	180	179.7	Organic matter. Very thin lamination.
103	180.1	180	Opaques.
104	180.3	180.1	Lignite.
105	180.5	180.3	Sublitharenite. Micas– opaques.
106	180.9	180.5	Lignite. (original sediments missing).
107	181.1	180.9	Sublitharenite with silty laminae of light gray color.
108	181.9	181.1	Sporadic organic matter. Lamination of 1 to 3 mm.
109	182.3	181.9	Lignite.
110	183.6	183	Sublitharenite. Organic matter– carbonized plant remains– quartz– opaques.
111	184.2	183.6	Lignite.
112	184.65	184.5	Very fine sand nodules– organic matter.
113	184.7	184.65	Lignite.
114	185.1	184.7	Very fine sand nodules– organic matter.
115	186.1	185.5	Abundant organic matter– thin lignite laminae.
116	187.1	186.6	Abundant organic matter– thin lignite laminae.
117	187.9	187.5	Lignite.
118	188.1	187.9	Organic matter– micas.
119	189.1	188.4	Micas– organic matter.
120	189.7	189.6	Thin lamination.
121	189.8	189.7	Sublitharenite. Micas– quartz– opaques– lithics.
122	190.1	189.9	Lignite.
123	191.1	190.3	Very fine black sand of indet composition.
124	191.9	191.6	Abundant organic matter and sulfur.
125	192.1	191.9	Lignite.
126	192.8	192.4	Organic matter– laminae 1 to 3 mm.
127	193.3	192.8	Sublitharenite. Organic matter– micas.
128	193.6	193.4	Sublitharenite. Organic matter and micas.
129	194.3	193.6	Lignite– with thin purplish mud laminae. (the bottom 40 cm are missing from the original sediments).
130	194.6	194.3	Organic matter and sulfur.
131	196.4	194.6	Thin planar lamination. Contains indet black fine to coarse sand grains in its matrix.
132	197	196.4	Quartz– micas– opaques– lithics.
133	197.7	197	Contains sand planar laminae.
134	198.5	197.7	Organic matter– lithics– micas and sulfur.
135	199.5	198.5	Bioturbation of millimetric traces. Stratification poorly preserved– planar to slightly wavy lamination.

136	200.9	199.5	Millimetric shells and traces– organic matter– opaques
and mica fragments.			
137	209.9	209.1	Sublitharenite. Organic matter– abundant micas and opaques.
138	213.3	209.9	Lignite. Very thin planar laminae of green to purplish mud– carbonized plant remains.
139	213.5	213.3	Organic matter– micas.
140	213.7	213.5	Lignite. Very thin planar laminae of purplish mud.
141	218.4	213.7	Lithic fragments– micas.
142	221.7	221.3	Lithic fragments– micas.
143	221.9	221.7	Organic matter.
144	224	221.9	Lithic fragments– micas.
145	224.5	224	Light organic matter.
146	225.5	224.5	Lithic fragments– micas.
147	226	225.5	Organic matter– color darkens towards base.
148	226.2	226	Lignite.
149	226.7	226.2	Abundant organic matter.
150	229.6	226.7	Fine to medium sand sized lithics– organic matter and sulfur.
151	230	229.6	Sublitharenite. Organic matter– very thin planar stratification.
152	231.4	230	Abundant organic matter– planar stratification.
153	234.9	233.5	Organic matter– has thin layers of gray mud laminae.
154	235.9	234.9	Thin laminae of 3 to 5 mm. Carbonized plant remains.
155	247	236.1	Thick homogeneous bed with few preserved structures.
Some thin planar laminae– 1 to 3 mm. Sporadic organic matter– poorly preserved and oxidezied. Very fine sand sized muscovite fragments. Slight color variation– with some 5 to 10 cm bands of yellowish–orangeish colors. Abundant globular oxides of dark red to black color– in two bands of ca. 20 cm at 244.2 m and 245.1 m. Sediments get slightly finer towards base– with sporadic organic matter.			
156	250.5	249.2	Organic matter– oxidized organic matter– carbonized plant remains.
157	252.4	250.5	Sporadic organic matter. Planar to slightly wavy lamination.
158	252.5	252.4	Siderite.
159	254.2	252.5	Sublitharenite. Organic matter– micas– opaques– lithics and quartz.
160	256.7	254.4	Sporadic organic matter.
161	257.1	256.7	Low oxidation.
162	258.1	257.1	Sublitharenite.
163	258.4	258.1	Sublitharenite.
164	264.2	261.4	Organic matter.
165	264.45	264.2	Organic matter.
166	272	270.55	Sublitharenite. Abundant quartz– lithics.
167	272.2	272	Oxidezied organic matter.
168	274.2	272.2	Sublitharenite. Abundant quartz– lithics.
169	277.7	276.6	Sublitharenite. Carbonized organic matter– opaques– lithics.
170	279.7	279.2	Bioturbated sublitharenite. Hardground.
171	284.2	283.05	Little organic matter.
172	289.8	289.5	Sublitharenite. Hard ground.
173	290	289.8	Organic matter.
174	292.7	292.55	Organic matter.
175	295.2	294.6	Little organic matter.
176	295.7	295.2	Sublitharenite.
177	297.9	296.2	Sulfur– organic matter– very thin laminae– carbonized plant remains.
178	298.2	297.9	Sublitharenite.
179	298.8	298.2	Little organic matter.
180	299.1	298.8	Thin lamination– some organic matter.

181	299.5	299.1	Lignite (impure)– with thin black mud laminae. Organic matter and sulfur.
182	305.35	299.5	Carbonized plant remains– red oxidation nodules. Sporadic sulfur– very thin lamina– 1 to 4 mm.
183	310.7	307	Sporadic organic matter– lithics of coarse to medium sand size. Sporadic micas (~1%)– discrete planar lamination.
184	313.5	311.05	Sublitharenite. Opaques (5%)– lithics (5%)– muscovite (~3%)– abundant quartz.
185	315.1	314.1	Sublitharenite. Quartz (85%)– lithics (10%).
186	317.6	317.1	Sublitharenite. Quartz (85%)– lithics (10%).
187	318.1	317.6	Little organic matter.
188	321.6	320.15	Sporadic organic matter. Very thin silty laminae– 1 to 2 mm.
189	322.7	321.6	Little organic matter.
190	323.3	322.7	Sublitharenite. Little organic matter.
191	324.2	323.3	Sporadic millimetric carbonized plant remains.
192	324.8	324.2	Organic matter
193	325.4	324.8	Lignite. Carbonized plant remains– sulfur.
194	325.6	325.4	Sulfur.
195	332.7	325.6	Very thin laminae– 1 to 2 mm– sporadic organic matter. Contains some very fine sand accumulations (<5 cm).
196	333.3	332.7	Quartzarenite. No organic matter.
197	334.8	333.3	Quartzarenite.
198	349.9	345.6	Sporadic very thin planar lamination.
199	353.2	352.7	Sporadic organic matter.
200	358.8	355.6	Laminated– little organic matter.
201	359.1	358.8	Peat. High content of organic matter– sulfur.
202	364.9	359.1	Sporadic organic matter. Thin planar laminae– <1 mm.
203	369.8	368.95	Sublitharenite. Silty matrix.
204	373.8	369.8	Organic matter– very fine sand sized quartz.
205	383.3	383.2	Quartzarenite.
206	391.6	389.3	Sublitharenite.
207	402.5	401.5	Sublitharenite.
208	404.8	404.55	Sublitharenite. Silty matrix– some opaques.

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